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# A NOTE ON SYMMETRY AS A FACTOR IN THE EVOLUTION OF PLANTS AND ANIMALS

FREDERIC T. LEWIS, M.D.

*Harvard Medical School, Boston, Mass.*

REPORTING AN ILLUSTRATIVE STUDY OF THE TRANSFORMATION OF THE AORTIC ARCHES IN THE SHEEP BY DR. GEORGE H. JACKSON, JR.

THE pretentiousness of this subject, even when qualified as a note, is greatly at variance with the simple nature of the observations to be presented. But simple and familiar as they are, they seem to be of considerable significance, and for the author, at least, have been of perennial interest.

Symmetry is here to be considered in the wide and non-mathematical sense of a balanced and harmonious relation of parts or organs, and as displayed in three main types—bilateral, radial, and spiral symmetry. In bilateral symmetry, which is the simplest form, the laws are, according to Bichat, that whenever an organ is beyond the median line it should be double; it should be simple, on the contrary, but regular, when it falls upon it.[1] Fixing his attention upon this one form of symmetry, so conspicuous in the disposition of the limbs in animals, and contrasting it with what seemed to him the wholly disorderly arrangement of limbs in trees, Bichat declared that in forming the plant "nature, one might say, has

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[1] Bichat, Xav., "Mémoire sur les rapports qui existent entre les organes à forme symétrique, et ceux à forme irrégulière," *Mém. de la Soc. Méd. d'Émulation*, Paris, An VII (1798–9), T. 2, p. 482.

forgotten her rule and compass." Radial symmetry, so prevalent in plants, but abundantly associated with both the other types, is a more complicated or higher form than the bilateral. For symmetry, as Jaeger has said, is a term to draw attention to a certain process of repetition manifest in a figure, its symmetry consisting in the regular repetition of its definite parts, so that by superimposing or otherwise, these parts may be made to coincide.[2] This principle he illustrates with a reference to the surprising and very beautiful symmetrical effects obtained in mirror-kaleidoscopes, due to the repeated reflection in regularly arranged little mirrors, of a number of insignificant pieces of glass thrown together by mere chance. In black and white he shows the same thing by a random scattering of dots in a wedge-shaped area, which needs only to be repeated in rotation, making this wedge the segment of a regular polygon, to produce a complex symmetrical pattern. "The splendor and fascinating beauty of a great number of living creatures," he declares, "are in each case caused by the mere action of symmetrical *repetition*." Since in bilateral symmetry there is but a single repetition, it may be regarded as simpler than the radial, which requires two or more.

In the radial arrangements of both animals and plants there is a certain preference for the pentamerous or pentagonal form, "which is the more remarkable," Jaeger comments (p. 61), "since this particular symmetry is quite impossible for crystalline matter." Thompson notes that Kepler in 1611 was seeking "an explanation of the mysterious and even mystical beauty of the five-petaled flower,"[3] and both Jaeger and Thompson review the extensive subsequent literature bearing upon its mathematical interpretation—a problem "not to be set and answered in a word."

The pentamerous whorl of plants is often clearly a condensed spiral, and spiral arrangements, so strikingly evident in the higher plants, are apparently more frequent in the viscera of the higher animals than is generally recognized. They may involve no repetition of parts, and then are a form of symmetry only in so far as they are an orderly and geometrical disposition of organs.

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[2] Jaeger, F. M., "Lectures on the Principle of Symmetry," 2d ed., Amsterdam, 1920, pp. 2–4.

[3] Thompson, D'A. W., "On Growth and Form," Cambridge, 1917, p. 480.

Symmetry in organisms is presumably the result of various tensions, diffusions, effects of gravity and other physical causes, with which the present morphological study is not at all concerned. Symmetrical arrangements may proceed from an even distribution or dispersal of blood or sap, which in turn they would favor, being thus serviceable arrangements; and they are often held to be expressions of equilibrium, mechanical stability and repose. But in organisms they seem difficult to maintain, so that departures from a symmetrical plan are frequent. If a new symmetrical relation is reached, or an approximation thereto, a new form may be produced of greater or less permanence. From the preponderance of symmetrical forms in nature, it may be assumed that there is a special tendency to produce them; and unsymmetrical arrangements, being relatively exceptional and apparently more variable, are perhaps transient, and destined to be replaced by new ones, more symmetrical and enduring. If this be true, a great range of future changes in the anatomy of plants and animals seems possible, some of which one might venture to predict. An instance will be cited where symmetry is so nearly attained that, due to superficial examination, it has been assumed already to exist. In other cases departures from primitive symmetry have been such that no symmetrical rearrangement seems ever possible. With such suppositions in mind it is proposed to examine two instances in which the factor of symmetry may be of controlling importance—first, in what seems the simpler matter, the floral variations in the genus Campanula; and then in a more complex problem in mammalian embryology.

## Floral Variations in Campanula

Campanula is a well-marked genus of more than a hundred species, several being very common in cultivation, growing chiefly in the temperate regions of the northern hemisphere. The Alps, Italy, Greece, the Caucasus and the Altai Mountains are, in De Candolle's expression, their native land, and in whatever direction one leaves it, the number of species promptly diminishes. Their flowers, in the symmetry of which alone we are interested, have normally a five-cleft calyx which is adherent to the ovary, a five-lobed bell-shaped corolla, five stamens, and either three or five stigmas associated with a corresponding number of carpels. The species with three carpels greatly predominate, outnumbering those with five by approximately ten to one.[4] It is hardly possible to know which of these arrangements is primary and gave rise to the other—the somewhat unsymmetrical form which is prevalent, or the less usual, perfectly symmetrical flower with all its parts in fives. The latter will be presented first, merely for convenience of description. Against regarding such flowers as primitive, Eichler has written the following vigorous protest ("Blüthendiagramme," Leipzig, 1875, Th. 1, p. 9):

> An example of unacquired heteromery, very frequent especially among dicotyledons, consists in this, that the pistil has fewer members than the preceding whorls—that it is "oligomerous." It has been attempted time and again to explain this by abortion from isomery (see, *e.g.*, A. Braun, "Verjüngung," p. 105; Wydler, in several places) yet in most cases there is no ground for such an assumption. Actual evidence is wholly lacking. One sees, for example, in the otherwise 5-merous flowers of the Apocynaceæ, Solanaceæ, etc., from the first no more than two carpels—of abortive ones, no trace—and placed in such position opposite each other that the theory making them the only two members to develop out of an original 5-merous cycle is clearly unjustified. That now and then a 3-, 4-, or 5-merous cycle actually appears, shows nothing more than that the number of carpels can vary, just as happens in the other

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[4] De Candolle, in his "Monographie des Campanulées," Paris, 1830, recognized 13 species with 5-locular capsules and 5 stigmas, and 124 species with 3-locular capsules.

whorls. Why under these circumstances one should insist on isomery is not to be understood. Were *all* the whorls of the same number, there would be some ground for the assumption; but when the leaf-arrangement at the base of the shoot usually begins with a lower divergence (the two bracts, placed at ½) there can be nothing strange in the idea that at the apex there is a falling back to a similar divergence.

A modification of Eichler's "floral diagram, or ideal section" of *Campanula medium,* a completely symmetrical form with five carpels, is shown in Fig. 1 *A*. In this species, where the sepals meet in the outer circle, there are certain appendages, shown in the diagram as loops. The petals alternate with the sepals, and the stamens with the petals. But the carpels or cells of the ovary are opposite, and not alternate with the stamens. In the midst of each carpel is seen the section of its *carinal vein* (or nerve), which in the actual flower extends upward as the midrib of the adherent sepal.

The unexpected failure of the carpels to alternate with the stamens has its explanations. After Brown had announced his opinion that the typical flower possessed two alternating rings of stamens, being "diplostemonous," De Candolle applied a similar idea to the interpretation of this campanula. He assumed that a cycle of alternating floral structures once existing between the present ring of stamens and the carpels had been suppressed, thus leaving the carpels opposite the stamens. But when he found that in two other species of what Linnæus considered Campanula, the arrangement of parts was precisely as in *C. medium* except that the carpels did alternate with the stamens, the hypothesis became somewhat involved. In these species the stamens stand opposite the ovarian septa, and thus they alternate with the carinal veins. Dumortier had already made the new genus Musschia for one of these species, and De Candolle proposed Platycodon for the other. But the explanation remains unsatisfactory, for as Penzig recently points out, among all the near allies of the Campanulaceæ there is actually no case of diplostemony; and Eichler, after considerable discussion, concludes curtly,—"The fact is, we have two sorts of carpel-orientation in the Campanulaceæ; how it is explained, the future may show, but the interpretations proposed hitherto are untenable" (*l. c.*, p. 296). A further suggestion as to its significance will be found in the following paragraphs.

In *C. medium* numerical variations of the sort which occur so freely in species with three carpels have not been as often or so carefully reported. Either they are less common because of the greater stability of the completely pentamerous flower, or the other more conspicuous abnormalities of this species have caused them to be overlooked. For *C. medium,* according to Heckel, has "become classic through the facility with which it produces double flowers formed of gamopetalous corollas enclosed one within the other," and alternating regularly. The calyx is often petaloid, and may be multiple; Heckel reported a terminal flower with three calyces and four corollas, but with normal andrœcium.[5] Fasciation of the stem is frequent, and of similar origin are the fused flowers with increased numbers of parts; but such monstrous forms belong in a different category from the numerical variations under consideration. In the Botanical Garden at Modena, Penzig saw a plant in which all the flowers were transformed into leafy shoots. On the elongated floral axis were many lanceolate leaves spirally arranged, and only at the tip there stood a whorl of three normal carpels with long stigmas.[6] Possibly this is a reversion to the primary number of carpels for the genus. In otherwise normal flowers of *C. medium,* the number of carpels may be reduced to four, or "accidentellement" to three, as stated by De Candolle, who thought that he had figured such a specimen, but it does not appear in his plates. Instead, we find a section of a 4-celled ovary here reproduced as Fig. 1 *f*. Its asymmetry is manifest in the distribution of the carinal veins, one cell having two veins in its wall, but the others only one.

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[5] Heckel, E., "Nouvelles monstruosités vegetales," *Bull. de la Soc. Bot. de France,* 1882, T. 29, p. 308–309.

[6] Penzig, O., "Pflanzen-Teratologie," 2te Aufl., Bd. 2, 1921, p. 534.

Before considering the variations in species with 3-celled ovaries, it may be noted that a 4-parted whorl forms a particularly disharmonious combination with one of five parts, whereas the association of 3-parted and 5-parted whorls more nearly approaches symmetry. The relations in these two combinations are shown in the diagrams Fig. 1 *D* and *E*, in which a circle of five anthers (such as might be sectioned in a campanula-bud) is shown in relation with 4-celled and 3-celled ovaries, respectively. The combination in Fig. 1 *D*, with a 5-parted corolla and calyx added, is not common in normal plants, but it occurs in Symphoricarpos and Parnassia, and is tolerated. Parnassia is said to have three and five carpels as variants, and the genera allied to Symphoricarpos have two, three, or five. The combination shown in Fig. 1 *E*, on the contrary, is very common. This is clearly associated with the fact that its whorls, showing respectively the 1/3 and 2/5 arrangements, are successive stages in the phyllotactic series, moving toward the "ideal angular divergence"; but the 1/4 arrangement of the carpels, as in Fig. 1 *D*, finds no place in that series. With the establishment of a 4-carpellate gynœcium, the loss of the fifth stamen, petal and sepal may be anticipated, producing a tetramerous flower with alternating whorls, the members in each cycle adjusting themselves to an angular divergence of 90°.

The parts in a tricarpellate campanula are placed normally as in the diagram Fig. 1 *B*. If a pentamerous flower is lateral and extends horizontally from the stem, the whorls of sepals and petals are usually so oriented that a sepal is directed upward, and a petal downward, in the midline.[7] The flower-stalk has two bracts, one on each side, which ordinarily lie in a horizontal line. In *C. rapunculoides* these bracts are sometimes nearly vertical, and a median sepal may be below instead of above. Eichler found that in the Campanulaceæ generally, a sepal, genetically the second one, is uppermost. He observed the reversed position "only exceptionally, yet not exactly rarely." "I found it especially frequent in Specularia, but it is nowhere normal; and if Hofmeister plainly states that the odd sepal in *C. medium* is median and

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[7] Brown, Robert, "Observations, etc., 1826," in Misc. Bot. Works, Ray Soc., 1866, Vol. 1, p. 291.

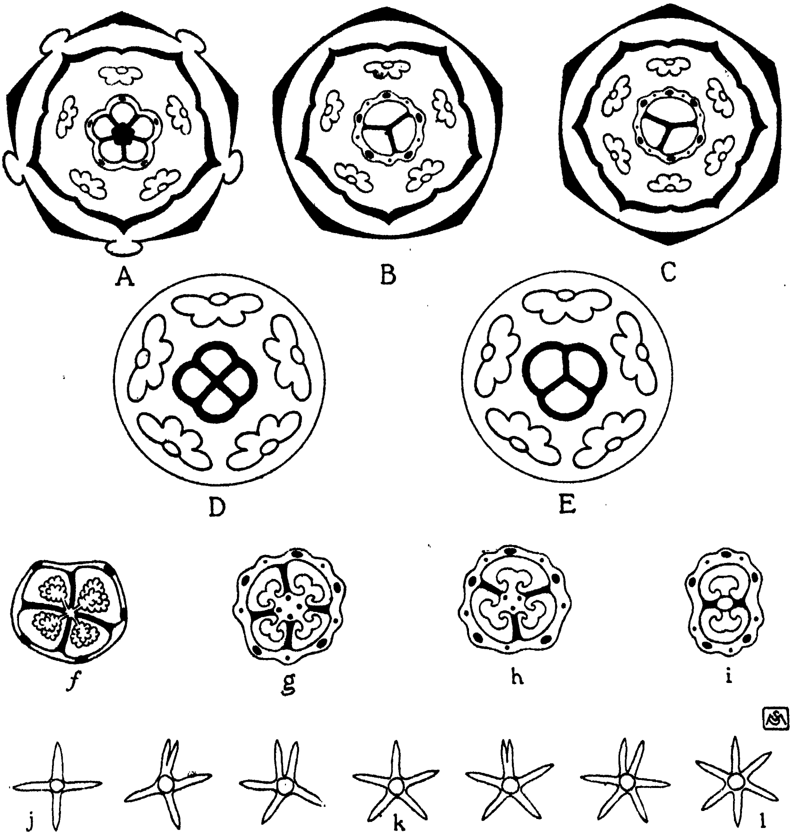

FIG. 1. *A*, diagram of the symmetrical flower of *Campanula medium* L. (modified from Eichler). *B*, diagram of the asymmetrical tricarpellate *C. rapunculoides* L. *C*, diagram of the nearly symmetrical tricarpellate hexamerous variant of *C. rapunculoides* L. *D* and *E*, diagrams of possible relations of the 4- and 3-carpellate ovary respectively to the 5-merous cycle of stamens. *f–i*, sections of ovaries showing the relation of the septa to the carinal and sutural veins: *f*, a 4-carpellate variant of *C. medium*, with carinal veins only (after De Candolle); *g*, *h*, and *i*, 4-, 3-, and 2-carpellate forms of *C. rapunculoides*. *j–l*, calyx-patterns of *C. rapunculoides*, varying from the normal (*k*) to the 4-merous form (*j*), and to the 6-merous form (*l*). (Except as otherwise stated all figures are from the author's sketches carefully redrawn by Mr. F. Schuyler Mathews.)

below, then I must contradict it."[8] Another variable feature is the orientation of the three carpels. Eichler finds that "ordinarily the odd carpel is upward (as in Fig. 1 *B*), but sometimes the reversed position occurs (Fig. 1 *E*)." In the allied genus Phyteuma, Wydler likewise found the unpaired carpel upward, or toward the main stem, "most frequently,—less often, median and below."[9] As shown in Fig. 1 *B*, the carpels may be of unequal size and not accurately oriented. The distribution of the veins in their outer walls is highly unsymmetrical. There are ten of these veins,—five carinal, which are continued as midribs of the sepals, and five, usually somewhat smaller, sutural veins (so designated by De Candolle), midway between the sepals and in line with the midribs of the petals. Since some of these veins arise as branches of the others in the lower portion of the ovary, it is only near the top that they become evenly spaced. Ordinarily one of the three carpels includes two carinal and two sutural veins; another has one carinal and two sutural; and the third has two carinal and one sutural. This distribution of veins is shown in *C. rapunculoides* (Fig. 1 *B*) and in a section from *C. rotundifolia* figured by De Candolle, and its marked asymmetry may well be correlated with the abundance of variations in these and allied species.

The asymmetry of the trimerous pistil is further emphasized by the arrangement of the hairs which beset the upper part of its style in ten longitudinal ranks. These ten rows of collecting hairs are evidently due, as De Candolle observed (*l. c.*, p. 18–21), to the close approximation, in the bud, of the five anthers to each other and to the style, around which they form a closed ring. As suggested in Fig. 1 *E*, the notches between adjacent anthers together with those in the midst of each anther form ten longitudinal grooves which offer the only available space into which the hairs may grow out.

Writers on monstrosities have found little of interest in the minor numerical variations of the tricarpellate campanulas, usually referring to them as "well known" when describing some great thing like a flower with 10,

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[8] Eichler, A. W., "Blüthendiagramme," Theil 1, Leipzig, 1875, p. 294.

[9] Wydler, H., "Kleinere Beiträge," Flora, 1860, Jahrg. 43, p. 594.

13, or even 30 petals. But Witte placed on record 22 different numerical combinations which he observed in *C. rotundifolia* growing in northern Sweden; and Dahlgren, also in Sweden, found in four species, 58 different combinations.[10] He records 7 others seen by Witte and Sylvén, of which he failed to find examples, and believes the list still incomplete; it includes no flower with as many as ten parts in any whorl. The special value of Dahlgren's tabulation is that it gives the number of examples which he saw of each form, though the thousands of normal flowers among which they occurred were not counted. Of *C. rapunculoides* he examined relatively few plants and found only 20 numerically abnormal flowers; of *C. rotundifolia* he has 277 variants, of *C. persicifolia,* 122; and of *C. patula,* 420—altogether 839 numerically abnormal flowers. These variations are summarized in Table I. The figures in each column indicate the number of instances the whorl named at the left contained the number of parts placed at the head of the column; that is, 9 flowers among the 839 variants had 3-parted calyces, 315 had 4-parted calyces, etc.; the total, in the right-hand column, shows that 568 of 839 variants were abnormal as to calyx. The table demonstrates that most variations consist merely in the addition or removal of one member of any whorl,—much less often, two members, and only rarely more than that. For some observers this is the

TABLE I

| | | 3 | 4 | 5 | 6 | 7 | 8 | 9 | |
|---|---|---|---|---|---|---|---|---|---|
| Sepals........ | 0 | 9 | 315 | – | 226 | 17 | 1 | 0 | 568 |
| Petals........ | 0 | 6 | 355 | – | 283 | 15 | 0 | 1 | 660 |
| Stamens...... | 0 | 6 | 330 | – | 228 | 10 | 0 | 1 | 575 |
| Carpels....... | 49 | – | 197 | 4 | 1 | 0 | 0 | 0 | 251 |

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[10] Witte, H., "Ueber abweichende Zahlenverhältnisse und einige andere Anomalien der Blüten der *Campanula rotundifolia* L.," *Arkiv för Botanik,* 1905, Bd. 4, N: o 17.

Dahlgren, K. V. O., "Studier öfver afvikande talförhållanden och andra anomalier i blommorna hos några Campanulaarter," *Ark. f. Bot.,* 1911, Bd. 10, N: o 10. For a translation of this paper, the writer is much indebted to Miss Ruth Berggren.

whole significance of these variations. With the carpels the tendency to increase rather than decrease greatly predominates in all four species. To a less extent the same tendency prevails in the outer whorls of *C. rotundifolia.* But the other species severally, and all four taken together as seen in the table, have a reduced number of sepals, petals and stamens more often than an increased number. The number of petals is somewhat more subject to variation than that of stamens or sepals, in Dahlgren's list. But the carpels are clearly the most fixed and conservative element in the flower, variations in any other whorl being more than twice as frequent. Even the stigmas vary more than the carpels, for Dahlgren found 50 flowers in which the number of stigmas and carpels did not agree, and in 46 of these the number of carpels was normal.[11] Witte previously had noted that a style with either two or four stigmas might proceed from a normal 3-celled capsule.

The appearance of some of the variants of *C. rapunculoides* is shown in Fig. 2, with a raceme of normal flowers at *A* (formula, or number of parts in the successive whorls, 5, 5, 5, 3). Symmetrical flowers may be produced by increasing the carpels and stigmas to five, the first step in the process being apparently the formation of four stigmas. In the three allied species Dahlgren found 28 flowers with four stigmas but only three carpels. Next would occur 4-carpellate, 4-stigmatate forms, of which he observed 104 examples (Fig. 2 *c*). Apparently the upper loculus of the 3-celled ovary usually widens (Fig. 1 *h*), and then becomes divided, with some readjustment of the septa, in making the four carpels (Fig. 1 *g*). The septa are rarely, if ever, placed with geometrical precision. The distribution of the carinal veins in the carpel-walls may be exactly like that in De Candolle's variant of *C. medium* (Fig. 1 *f*). Such flowers presumably represent the stages traversed in making the antisepalous form of the completely symmetrical pentamerous campanula, and thus the evolution of a distinct section of the genus seems primarily a matter of symmetry. Dahlgren found one 5, 5, 5, 4 flower of *C. patula* with 5 stigmas, and two flowers—one of that species and one *C. rotundifolia*—which were completely pentamerous. The unstable forms with formula 5, 5, 5, 4, though common variants, are apparently not normal for any species of Campanula, nor characteristic of any related genus.

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[11] The flowers with 5 sepals, petals, and stamens, and 3 carpels, but with an abnormal number of stigmas, have not been included in the above tabulation. There were 33 of these.

It seems not improbable that species with five carpels alternating with the stamens (and so opposite the petals, or "antipetalous") were likewise derived from tricarpellate flowers by a different arrangement of the septa, rather than by the suppression of a hypothetical circle of stamens. For the septa may extend either to the carinal veins (note the upper septa in Fig. 1 *h*) or to the sutural veins (as below in Fig. 1 *g*). If all the septa should be of one or the other of these types, the flowers would become antipetalous or antisepalous accordingly. Again, the lower right carpel in Fig. 1 *B* is almost perfectly antipetalous. The others need only become like it to produce flowers generically distinct from the form in Fig. 1 *A*. Or, should the arrangement of the three carpels in Fig. 1 *B* be inverted, as sometimes happens, and the median lower cell enlarge and subdivide as the median upper one seems to do normally, then the carpels would be antipetalous. In fact, five such antipetalous carpels may actually be produced as variants of *C. persicifolia*, according to Penzig (*l. c.*, p. 537). It appears, therefore, that the evolution of the antipetalous pentacarpellate genus Platycodon, like that of the antisepalous pentacarpellate species of the *C. medium* type, is essentially the attainment of symmetry from or through the tricarpellate form.

A different sort of symmetrical flower, not found normally in any species of Campanula, but representing what may perhaps, at some future time, be specifically distinct, occurs as a common variant of *C. rapunculoides*. Among some plants growing without cultivation around a long-abandoned garden, the writer found, in 1896, that in 31 out of 367 flowers examined, there were 3 carpels, 6 stamens, 6 petals, and a more or less 6-parted calyx, the flowers being quite symmetrical on the plan of three (Fig. 1 *C*). Later some twenty more such flowers were found, including the stalk in Fig. 2 *B*, which bears seven of them. It has also—the second from below—a 6, 6, 6, 4 form. The lowest bud is 6-parted; four others are 5-parted and one—the fourth from the top—is 4-parted. It seems a general rule that the lower flowers may be 5-parted; then, and often with some variations, the 6, 6, 6, 3 form is attained and held; with finally, toward the top of the stem, a falling off to the pentamerous form. Certain individual plants or groups of plants show this tendency, sometimes to such an extent that 6, 6, 6, 3 flowers predominate. The increase of parts may begin in the calyx, a lobe of which, and apparently not always the same one, becomes split. The parts diverge and the other sepals become rearranged to make an even 6-pointed star (Fig. 1 *k-l*). Meanwhile the stamens and petals have added a member, sometimes in advance of the calyx. Dahlgren found in the four species the following combinations: 6, 5, 5, 3–15 flowers; 6, 6, 5, 3–26 flowers; 6, 6, 6, 3–109 flowers. But he found also 5, 6, 5, 3–19 flowers; 5, 6, 6, 3–37 flowers; which indicate that the initiative is somewhat more often in the corolla than in the calyx. No flower was found of the formula 5, 5, 6, 3, so that the stamens are clearly not an active factor.

The flowers of the formula 6, 6, 6, 3 prove to be, on section of the ovary, not as symmetrical as might be expected. Usually one cell is much the largest, and may contain six of the twelve veins in its wall (Fig. 1 *C*). Although cells nearly equal in size have been seen, in no case have the septa passed symmetrically to three carinal or three sutural veins. But such flowers may yet be found, since the requisite readjustment is sometimes slight. Probably correlated with the width of the upper carpel there is a tendency for the 6-parted flowers to produce four carpels, one instance of which has already been noted. Dahlgren found 51 of these flowers. If two opposite carpels should be antipetalous and the other two antisepalous, a remarkably symmetrical form would result, but such perfection has not been observed. A single flower of the 6, 6, 6, 5 pattern was found by Dahlgren, but not one with all its parts in sixes, as is characteristic of the campanulate genus Canarina. That coarse aberrant form, of the Canary Islands, is, however, often pentamerous, and from such a type it presumably developed. Often *C. rapunculoides* and its allies go beyond the hexamerous arrangement, producing a wide scattering of unsymmetrical combinations. Of these the most frequent is probably 7, 6, 6, 3, of which Dahlgren saw five examples. Witte describes a single plant of *C. rotundifolia* in which 28 out of 32 blossoms were abnormal, and 14 of them had gone beyond 6, 6, 6, 3 to 7, 6, 6, 3; 7, 7, 6, 3; 7, 7, 7, 3; 8, 6, 6, 3, etc. It appears very strikingly in Dahlgren's table, however, that most of these higher unsymmetrical combinations are represented, among the 839 variants, by single specimens only, and none by more than five cases. There is no record of a completely 8-merous flower, with 8 carpels and 8 stigmas, such as is normal in the small campanulate genus Michauxia. It may be regarded as an indication of a recently acquired and difficult symmetry that the flowers of Michauxia are notably subject to numerical variation (Penzig).

Having considered the ways in which the asymmetrical tricarpellate campanulas may and do acquire symmetry by the increase of their parts, there remain to be presented the variations involving reduction. Rather unfrequently in *C. rapunculoides* the carpels and stigmas are reduced to two in an otherwise normal flower (Fig. 2 *d*). The carpels are usually placed one above the other, each having five veins in its wall and being to this

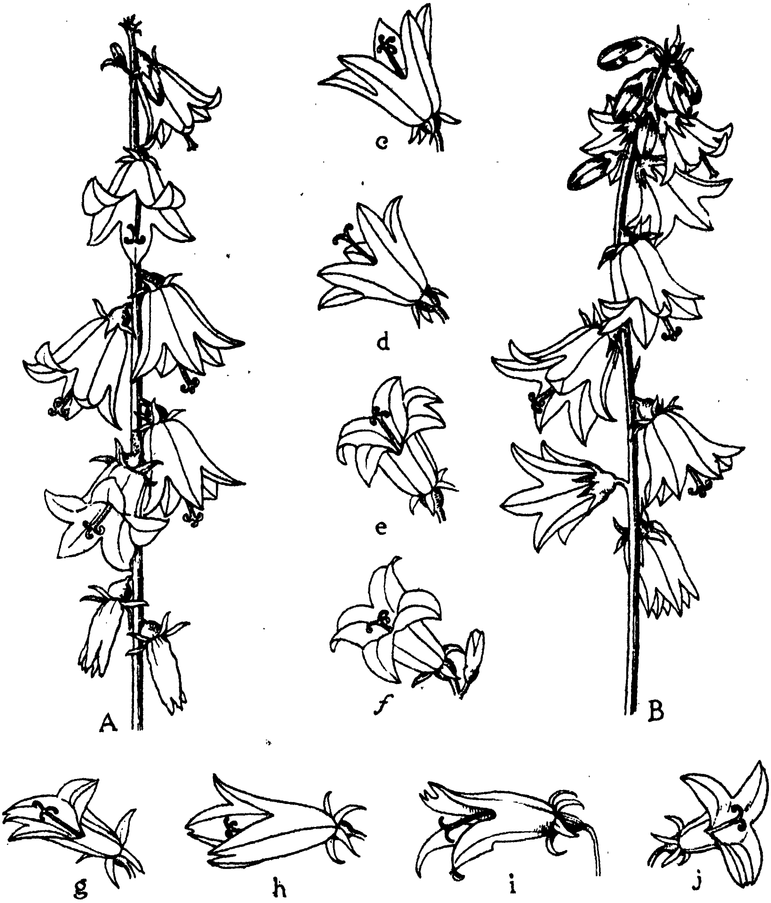

FIG. 2. Numerical variations in the flowers of *C. rapunculoides*. *A*, normal 5, 5, 5, 3 flowers; *B*, the nearly symmetrical 6, 6, 6, 3 variant; *c*, the 5, 5, 5, 4 form; *d*, 5, 5, 5, 2; *e*, 5, 5–4, 5, 3; *f*, 4, 4, 4, 3; *g*, one wide and three normal sepals, 2-tipped corolla, 5 stamens, 3 stigmas; *h*, 5 sepals, tripartite corolla, 5 stamens, 3 stigmas; *i* and *j*, 5, 5, 5, 2 flowers with corollas suggestive of lobelia, the broad 3-toothed segment of the corolla being above in *i*, and below in *j*. (Drawn by Miss Mabel Herford, except *i* which is by Mr. H. F. Aitken.)

extent symmetrical (Fig. 1 *i*); but they generally vary in size and their axis may be at an angle with the vertical. Dahlgren records 18 flowers with the formula 5, 5, 5, 2. It is a change taking place in the allied genus Phyteuma, in which De Candolle described 15 species with 3 carpels; 10 species with "3, sometimes 2," or *vice versa;* and 3 species with 2 stigmas and bilocular capsules. In another allied genus, Jasione, the species are all of the 5, 5, 5, 2 type.

More frequently, in the campanula-variants, the members of the outer whorls are reduced to four, while the three carpels remain unaltered. In producing flowers of the 4, 4, 4, 3 type (Fig. 2 *f*) two petals may fuse, as in Fig. 2 *e,* and the calyx may show such intermediate stages as in Fig. 1 *k–j.* Of what may be regarded as stages in its production, Dahlgren records the following combinations, here followed by the number of flowers of each kind which he observed; 4, 5, 5, 3–29; 4, 4, 5, 3–7; 5, 4, 5, 3–14; 5, 4, 4, 3–39; but no instance of 5, 5, 4, 3. As with the increase in the outer whorls, the initiative is never with the stamens; it is often with the calyx, but distinctly more often with the corolla. The resulting unsymmetrical flower (4, 4, 4, 3) not normal for any campanulate species or genus, Dahlgren found to be the commonest variant, yielding 247 examples. It becomes symmetrical when the carpels are reduced to two, but only fifteen such flowers were found. Further reductions lead to the form 3, 3, 3, 2, of which a single example is listed, but as shown in one of Dahlgren's figures, the trimerous corolla may be perfectly formed, without bifid lobes or other evidence of its pentamerous derivation. In the related genus Wahlenbergia, which has been called the Campanula of the southern hemisphere, there are some completely pentamerous species and many of the 5, 5, 5, 3 type, but in *W. lobelioides* the features of the variant just described have become specific characters. De Candolle (*l. c.,* p. 158) says of *W. lobelioides:* "The calyx-lobes are often 3 but sometimes 4 or 5; their number seems to be greater in earlier flowers. The corolla, usually 3-cleft, but sometimes 4- or 5-cleft, varies less than the calyx. I have found the stamens always 3, and the cells of the capsule 2." But this is neither a very symmetrical nor a very stable arrangement.

Some reduced forms of *C. rapunculoides* are shown in Fig. 2 *g–j,* all of which came from a small group of uncultivated plants on the site of the Boston Lying-in

Hospital. No such flowers were seen during several years in another patch which yielded many 6, 6, 6, 3 blossoms, and they probably are quite unusual. Magnus has noted that polymerous flowers of other campanulas are "not rare in certain localities,"[12] but what leads to the local production of particular variants is past speculation. The distorted flower in Fig. 2 *g* has 3 stigmas, 5 stamens, a somewhat bilabiate corolla (due to the fusion of 2 and 3 petals, respectively), and a 4-cleft calyx. The tripartite corolla of Fig. 2 *h* results from the fusion of two pairs of adjacent petals, one petal remaining separate. This flower had 3 stigmas, 5 stamens, and 5 sepals. Another flower, not drawn, of the 5, 5, 5, 3 formula, had a tripartite corolla with the three lower petals fused and the two upper ones separate. Tripartite corollas were found also in three flowers with two stigmas. In one of these the segment of the corolla formed by the fusion of three petals was above, as the flower extended out from the stem (Fig. 2 *i*); in the other two it was below. These two differed as to their stigmas, which were transversely placed in a flower not drawn, but were nearly vertical in the other (Fig. 2 *j*). This flower has acquired essentially the form and bilateral symmetry of Lobelia, which, as exemplified in *L. inflata*, is illustrated in Fig. 3.

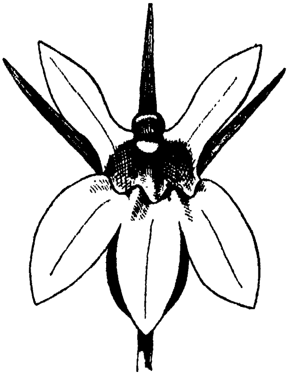

FIG. 3. The symmetry of *Lobelia inflata* L. Enlarged 6 diameters. (Author's sketch redrawn by Mr. Aitken.)

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[12] Magnus, *Verh. d. bot. Vereins d. Prov. Brandenburg*, Jahrg. 18, Sitz.-ber. vom 28 Juli, 1876, p. 111.

Notwithstanding the great difference in the form of flowers of Campanula and Lobelia, it has long been recognized that these genera are very closely allied. Jussieu placed them both in the Campanulaceæ in his "Genera Plantarum" of 1789, where Robert Brown left them, after extracting the "Stylideæ" and "Goodenoviæ" in 1810. They remain together in the Campanulaceæ of Schönland (Engler u. Prantl, Pflanzenfamilien, 1894). In Lobelia, apart from the different symmetry of the flower, the anthers have fused with one another in a ring about the style; and on one side, between two petals, the corolla is split its whole length. But the anthers of Campanula stand close together in the bud, and are somewhat fused in Jasione, and fully fused in three species which De Candolle removed from Campanula to his genus Symphandra. A corolla split down one side occurs as a variation in an otherwise normal flower of *C. rotundifolia,* well figured by Witte, and Dahlgren shows other instances. A further distinction between Campanula and Lobelia, first pointed out by Brown, is that the flowers of Lobelia in the bud take a very unusual position, by having a median sepal below and a petal in the midline above; but when these buds have opened, the flower stalk has twisted and the flower has been rotated to the usual position, with a median sepal uppermost. There seems to be some twisting in Campanula, but nothing as definite and pronounced as the "resupination" of Lobelia. It appears, therefore, that the flower in Fig. 2 *h* may be more like a lobelia than that in Fig 2 *i,* neither stem showing obvious twisting.

In reviewing what has been said of variations in Campanula, we are persuaded that symmetry is the expression of factors dominant in evolution. The principal types centering about the imperfectly symmetrical and consequently very variable tricarpellate campanulas are attainments of more symmetrical and sometimes more stable forms. Of these there have been mentioned the antisepalous pentamerous type of *C. medium;* the antipetalous pentamerous Platycodon; the hexamerous Canarina and octamerous Michauxia; the symmetrical 6, 6, 6, 3 form not as yet characteristic of any species; the 5, 5, 5, 2 type in Phyteuma and Jasione; and finally the rearrangement of the lobes of the corolla in that type, with the attainment of bilateral symmetry. This in some early group of campanulaceous plants was a momentous event in botanical evolution, leading to the lobelias and thence to the Compositæ, and changing in some seasons and places the entire aspect of vegetation.

If this interpretation seems too inadequate and overborne by the innumerable exceptions to symmetrical productions, is it not more simple and intelligible than to derive bilateral flowers from the radial "through a long course of slow modification,—each modification having been preserved which was useful to the plant?" Certainly Darwin's alternative is not strengthened when Spencer defends it as follows ("Principles of Biology," 1867, Vol. 2, Ch. X):

> If we bear in mind the functions of flowers, we shall find in their adaptations to their functions, under conditions that are extremely varied, an adequate cause for the different types of symmetry. . . . We shall find reason for concluding that the forms and positions of those subsidiary parts which give general shape to the flower arise by the survival of individuals which have the subsidiary parts so adjusted as to aid in the process of fertilization—the deviations from radial symmetry being among such adjustments. . . . So long as the axis of a flower is vertical, a bee or butterfly alighting on it will be as likely to come from one side as from another. . . . But a bee or butterfly coming to a laterally-growing flower . . . almost of necessity settles with the axis of its body inclined upwards towards the stem of the plant. . . . We see that a long undermost petal or lip by enabling the insect to settle in such a way as to bring its head opposite the opening of the tube, aids its fertilizing agency. But whatever be the special modifications of the corolla which facilitate the actions of the particular insects concerned, all of them will conduce to bilateral symmetry.

To ascribe the production of the bilateral flower in Campanula to the direction of the approach of bees is perhaps as diverting as anything in medieval physiology and supports Russell in doubting whether the whole theory of natural selection is properly applicable to problems of form.[13]

## SYMMETRY IN THE AORTIC ARCHES

After having seen in Campanula, and in other plants, the passage from one form of symmetry, through an intermediate asymmetrical condition, to symmetry of a new sort, some example of a similar process was sought in mammalian development. The transformation of the aortic arches in the sheep seemed to be an instance of this

[13] Russell, E. S., "Form and Function," London, 1916, p. 232.

kind, and the critical stages having been selected, Dr. G. H. Jackson, Jr., made a series of models of the vessels, drawings of which will here be presented. The labor and skill required were considerable, and the results show more extraordinary migrations of blood-vessels than have hitherto been recorded. For the privilege of presenting this story, the author is greatly indebted to his collaborator, Dr. Jackson. The drawings (Figs. 4–7) are all ventral views, in which the observer is looking at the arteries in the front of the thorax and neck.

At a certain stage in embryonic development in mammals generally, the blood leaves the heart by two more or less median ventral vessels, the aorta and pulmonary artery (Fig. 4, ao. and a. p.). From them the blood is conveyed to the back of the body by a series of bilaterally symmetrical arched vessels known as the aortic arches, and these empty into two longitudinal trunks, one on either side,—the dorsal aortæ (Fig. 4, ao. d.). The dorsal aortæ unite in the midline below, giving off the subclavian arteries, to the front limbs, shortly before their union. The pulmonary artery divides into the two pulmonary arches, from each of which a vessel descends to the corresponding lung. The aorta divides, somewhat indirectly, into two aortic arches on either side, which are known as the third and fourth arches, respectively. Anterior to them, in earlier stages, were the first and second arches which have now disappeared. The dorsal aortæ are continued up the neck as the internal carotid arteries; and ventrally, from the root of each third arch, an external carotid artery likewise passes up the neck. Except where the aorta and pulmonary artery leave the heart, this system of vessels is strikingly symmetrical, with a symmetry characteristic of the corresponding arteries in adult fishes. In mammalian embryos this pattern, with slight variations, everywhere prevails. But it gives rise to a great variety of arrangements in the adult, some of which are symmetrical or nearly so, but others are far from symmetry. With the growth of the sheep embryo, and the great elongation of the thoracic and cervical regions, the original symmetry is soon lost.

In the sheep of 14 mm. (Fig. 5), by comparison with the younger stage (10 mm.), the following changes may be noted. The subclavian arteries now leave the dorsal aortæ much higher up than before—the distance from their origin to the place where the dorsal aortæ come together below is now considerable. Moreover, the part of the right dorsal aorta between the subclavian artery and the aortic junction has been reduced to a strand, and in the next stage will have disappeared altogether. After that has taken place, the right dorsal aorta from the fourth arch to the origin of the subclavian artery is considered a part of the right subclavian artery. The right pulmonary arch has gone already, except as it is represented by the bend in the root of the branch to the right lung. The fourth arches have become very short and are no longer opposite each other, since on the right the confluence of the third and fourth arches with the main aorta has been drawn out and directed upward. The passage from the fourth to the third arch on either side has become greatly elongated, but more so on the left, and the resulting vessels may now be called the common carotid arteries. Each of them divides into the external carotid artery and the third arch, which arch, from now on, constitutes a part of the internal carotid artery. From the internal carotid artery proper to the fourth arch, the dorsal aorta on either side has become very long and slender; with its total disappearance in the next stage, the picture becomes greatly simplified.

At 18 mm. the arterial trunks of the sheep have the very unsymmetrical arrangement seen in Fig. 6, in which the following changes have taken place. The branches of the pulmonary artery to the right and left lungs now leave the pulmonary arch by a common stem, presumably an elongation of the place of their adjacent origin. The left subclavian artery has traveled up, beyond the pulmonary arch, to the root of a vessel marked "*x*," which deserves particular attention. It is a long main trunk prolonged from the region "*x*" of the preceding stage. Since it divides into vessels for the arm and head, it is named the brachiocephalic artery, but at this stage the vessel for the left arm, although at its root, is still independent. The way in which the left subclavian artery has moved along the aorta to its new position is quite remarkable, and seems due to a rearrangement of cells around its orifice, spreading apart above and closing in below. The common carotid arteries

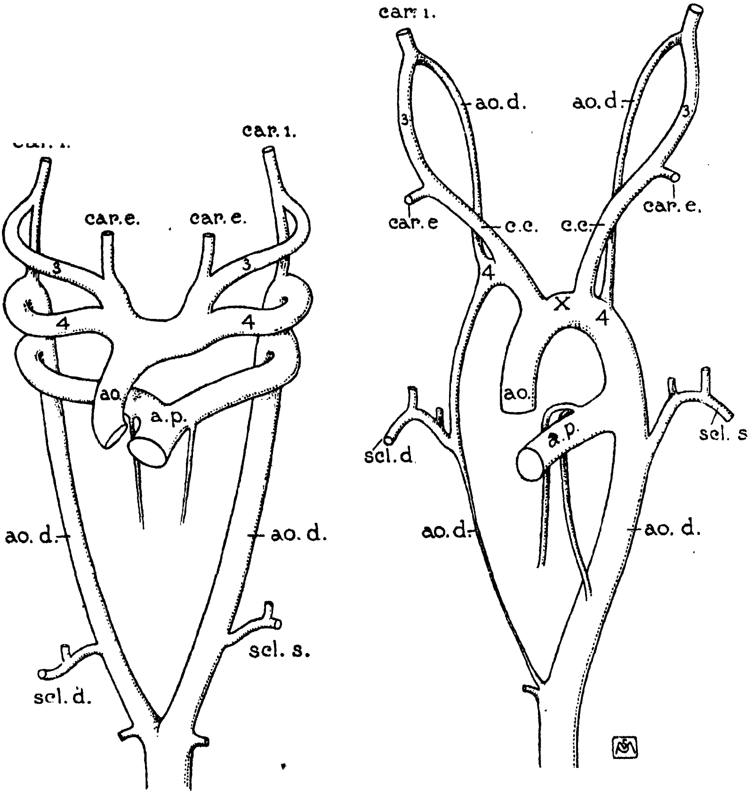

Fig. 4 Fig. 5

FIGS. 4–7. The development of the aortic arches of the sheep as seen in ventral view. Fig. 4, embryo of 10 mm. (Harvard Embryological Collection, Series 1232). Fig. 5, embryo of 14 mm. (H. E. C., Ser. 1106). *Ao.*, arch of the aorta as it leaves the heart; *ao. d.*, dorsal aorta; *a. p.*, pulmonary artery; *car. e.*, external carotid artery; *car. i.*, internal carotid; *c. c.*, common carotid; *scl. d.*, right subclavian artery; *scl. s.*, left subclavian; *3* and *4*, third and fourth aortic arches. *x* and *v* mark corresponding vessels in the successive figures, as explained in the text.

have become very long, and their bifurcation into external and internal carotids is now far up the neck. With the disappearance of the dorsal aorta on the right, the fourth arch has become an unrecognizable part of the right subclavian artery (at the position marked 4); the

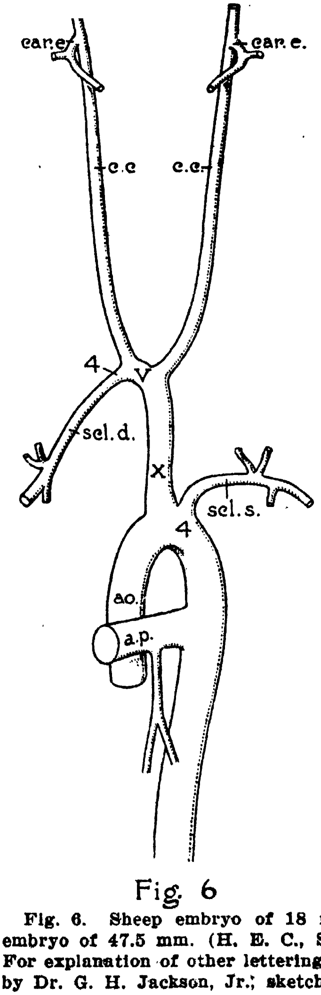

Fig. 6

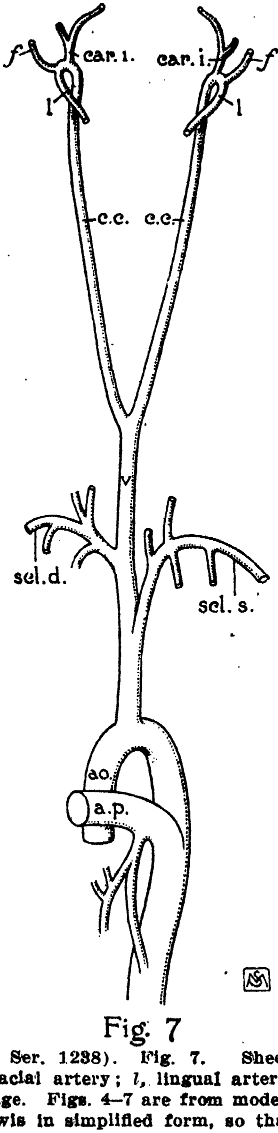

Fig. 7

Fig. 6. Sheep embryo of 18 mm. (H. E. C., Ser. 1238). Fig. 7. Sheep embryo of 47.5 mm. (H. E. C., Ser. 1696). *f*, facial artery; *l*, lingual artery. For explanation of other lettering, see opposite page. Figs. 4–7 are from models by Dr. G. H. Jackson, Jr.; sketched by F. T. Lewis in simplified form, so that the following magnifications are only approximate. Fig. 4, × 35 diam.; Fig. 5, × 30 diam.; Fig. 6, × 25 diam.; Fig. 7, × 8 diam.

left fourth arch is merged in the main arch of the aorta, without demarcation, presumably at the place likewise marked 4.

In such large sheep embryos as shown in Fig. 7 (47.5 mm.), a new symmetry has almost been attained, if the origin of the vessels from the heart be disregarded. A median brachiocephalic artery extends up the neck, along which the left subclavian artery has climbed to a point nearly opposite the right subclavian. This is followed by a median vessel "*v*," sometimes called the "cephalic" or "bicarotid trunk," which divides into the two common carotid arteries. It has been extended from the region "*v*" of the preceding stage. Each common carotid divides into the small internal carotid arteries and the very short external carotids; the latter divide at once into facial and lingual branches (*f* and *l*), which were seen in the preceding stage. This entire arrangement stops just short of the attainment of symmetry, for in the adult there is usually an interval, sometimes half an inch, between the points at which the subclavian vessels leave the brachiocephalic trunk. The slight shifting which would eliminate this interval would lead to perfect symmetry, far removed from that equally perfect symmetry from which it came.

The principal types of origin of the mammalian subclavian and carotid arteries from the arch of the aorta are shown in the diagrams in Fig. 8, which include all the symmetrical forms, *A*, *D*, *E* and *F*, with two quite unsymmetrical,—*B* and *C*. Similar diagrams are found in many books, but the best account of the occurrence of the various patterns is perhaps that of Parsons.[14] He writes: "I have for a good many years wondered what cause or causes determined the various arrangements of the great trunks arising from the arch of the aorta," and to find this out he dissected extensive zoological material and studied the literature. He decided that "nearness of kin does not seem to play any great part in determining the arrangement of these branches" and comments on the wide variation within a single species. "The commonest mammalian arrangement," he finds, "is that in which the left carotid rises from the base of the innominate"—a form intermediate between Fig. 8 *B* and *C*, the left carotid having fused with the innominate only low down and sufficiently to provide a common outlet. "From this," he declares, "the variations range in two directions, either toward concentration or separation of branches." Embryologically, however, the form in Fig. 8 *C* is more primitive, representing as it does an arrest of development at the stage of Fig. 5. It can, therefore, more logically be regarded as the center of divergent variations. This arrangement, with greater or less distance between the left subclavian and the left common carotid, is found, according to Parsons, in ornithorhynchus and echidna, in some marsupials (*e.g.*, the wombat), some edentates (armadillo and pangolin), in the dugong, in the beaver and occasionally in rabbits, in seals (but not in other carnivora), in several of the insectivora, sometimes in various monkeys, and as the normal arrangement in man. The variations in monkeys and in man have been tabulated by Sir Arthur Keith,[15] in whose judgment they form a series *progressing toward* the typical human arrangement (Fig. 8 *C*), which we regard as primitive and a point of departure.

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[14] Parsons, F. G., "On the Arrangement of the Branches of the Mammalian Aortic Arch," *Journ. of Anat. and Physiol.*, 1902, Vol. 36, p. 389–399.

An interesting symmetry may be attained if, beginning at the stage of Fig. 5, the left subclavian vessel should travel up the left common carotid artery to a point opposite the right fourth arch. Development without further changes would produce the arrangement in Fig. 8 *D*. This is acquired in certain of the insectivora. It is ascribed to the mole (Talpa) without exception. Parsons records it in one out of two golden moles (Chrysochloris) and in one out of three hedgehogs, the others having the primitive arrangement of Fig. 8 *C*, which is the only distribution attributed to certain other species, such as the desman (Myogale). In the bats "all authors seem agreed that the symmetrical bi-innominate arrangement is the constant one," and among cetaceans, insufficiently investigated, Parsons finds it "very common if not the commonest" distribution. It was found once as an anomaly in the chimpanzee,[16] and may occur in man, Poynter citing nine recorded cases.[17] Kopsch, in Rauber's Lehrbuch, 1906, states that the formation of two innominate trunks is "the most frequent variation" (in man) but this is contrary to all opinion. Wherever it occurs, it affords a perfect instance of the passage from one symmetry to another through an intermediate stage of disorganization.

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[15] Keith, A., "The Modes of Origin of the Carotid and Subclavian Arteries from the Arch of the Aorta in Some of the Higher Primates," *Journ. of Anat. and Physiol.*, 1895, Vol. 29, p. 453–458.

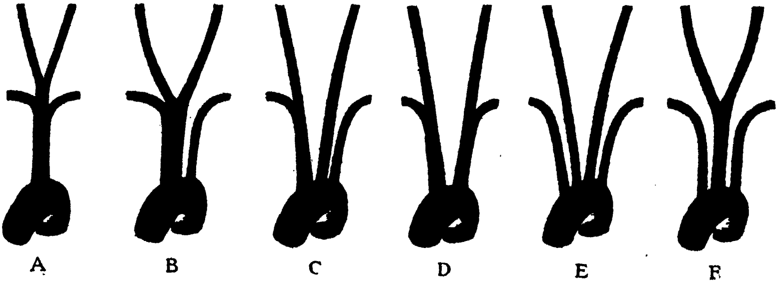

FIG. 8. Diagrams of the origin of the subclavian and carotid arteries from the arch of the aorta in adult mammals. *A*, the type already shown in Fig. 7. *B*, approximately a persistence of the stage in Fig. 6. *C*, arrest of development at the stage of Fig. 5. *D*, *E*, and *F* (with *A*) represent the symmetrical arrangements sometimes attained, as described in the text.

The great majority of mammals start toward that type of symmetry nearly attained in the sheep. The first step is the slight fusion of the left common carotid artery with the innominate, "man's commonest abnormality," according to Parsons, with a frequency of 1 in 10. It is normal for the rabbit and guinea pig. With greater fusion, extending almost, but not quite, to the level of the right subclavian, it corresponds with an arrest of development at the stage shown in Fig. 6. With slight variations this may give rise to three adult forms. The brachiocephalic artery may divide into a very short innominate and a left common carotid (form *a*,—Fig. 6); or the brachiocephalic may divide at once into three terminal branches (form *b*,—Fig. 8 *B*); or a slight median extension may produce a short bicarotid artery (form *c*). The distinction between the aforesaid forms *a* and *c* is carefully drawn by Parsons, though it seems to be without special significance. Of the kangaroo Macropus, two specimens were of form *a* and one of form *c*; the lion and ocelot have form *a*, and the tiger and leopard, form *c*. Some rodents and some monkeys present these arrangements, which, however, are specially characteristic of the carnivora and the pig; with a long bicarotid added, Fig. 8 *B* would represent the condition in the llama and giraffe.

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[16] Chapman, H. C., "On the Structure of the Chimpanzee," *Proc. Acad. Nat. Sci.*, Philadelphia, 1879, p. 57–58.

[17] Poynter, C. W. M., "Arterial Anomalies Pertaining to the Aortic Arches," *University Studies*, Lincoln, Nebraska, 1916, Vol. 16, 116 pp.

The final stages toward the symmetry of the sheep (Fig. 8 *A*) are, first, those in which the left subclavian begins to climb the brachiocephalic trunk. Such beginnings were found by Parsons in a few rodents (as the agouti) and sometimes in the genet (the only instance in the carnivora), but in these orders progress toward symmetry stops at that point. This initial stage is recorded also for the rhinoceros, gazelles, and antelopes, and in a single lemur among twelve (the others forming a progressive series from the type of Fig. 8 *C* through that of Fig. 8 *B*). The sheep, goat, and cow reach the form shown in Fig. 8 *A*, which is nearly attained in the horse.[18] But, as already noted, no careful description indicates that the two subclavian arteries are ever placed at exactly the same level.

The other symmetrical displays (Fig. 8 *E* and *F*) have been well illustrated in human anomalies, but are very exceptional as normal arrangements. Keith regards Fig. 8 *E* as "the natural climax" of the series in the higher Primates. It doubtless arises at an early stage (Fig. 4) by a deepening of the ventral cleft between the right third and fourth arches, followed by an arrest of development. Parsons found it once in the marsupial bear (Koala), but he does not record it for cetaceans as is often done. The form in Fig. 8 *F* has been found in the marsupial wolf of Tasmania, and by Cuvier in an elephant, but the elephant is said usually to have the arrangement in "man's commonest anomaly," namely an innominate joined at its base by the left common carotid. It seems unprofitable to speculate concerning its development, but the deepened ventral cleft in the stage of Fig. 4 would separate the right subclavian artery, and a subsequent elongation of the region "*x*" in Fig. 5 would produce a bicarotid vessel.

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[18] The primitive arrangement (Fig. 8 C) may be expected in these animals as anomalies. A perfect example, in a donkey, was reported by Huytra as cited by Skoda (*Anat. Anz.*, 1912, Bd. 40, p. 542, Fig. 5).

Before concluding that symmetry is the objective of all the variations which have now been presented, certain other interpretations must be considered. Concerning that "commonest variation in man" which we have regarded as a first step toward the symmetry of ruminants, less advanced than that taken by some monkeys, Sir Arthur Keith has said: "It is doubtful if one can legitimately construe this apparently cynomorphous reversion in Man as an atavistic tendency"—with which we fully agree, but he continues,—"more probably it has no more morphological worth than the degree of interdigital webbing." Although he thus makes the variations within a species of no moment, he believes "that the type prevailing in each genus in all probability best serves the body-economy of that genus, but how it does so is by no means clear." Since the frequent radical departures from the prevailing type occur without apparent detriment to the individual, this becomes an interesting profession of faith. As suggesting the way in which a particular plan of branching may be most appropriate for a given species, there is little to be added to Professor Owen's comments, in 1868, here quoted with references to our own figures whenever appropriate.[19]

> In the non-claviculate narrow-chested Ungulates the varieties *A* and *B* (Fig. 8) are met with, that of *A* prevailing: in non-claviculate but broader-chested Unguiculates, with flexile and rotatory fore limbs, the separate origin of the left brachial is more constant and remote from the innominata: the same is better marked in the broader-chested Swimmers (*Lutra, Phocœna*) and in the claviculate

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[19] Owen, R., "On the Anatomy of Vertebrates," Vol. 3, 1868, p. 537.

*Quadrumana:* in many *Insectivora* an analogous but other arrangement prevails (Fig. 8 *D*). In the broad-chested species illustrating the variety *C,* the head and pectoral limbs are supplied by three primary trunks: in the still broader and flatter-chested *Sirenia* the heart itself is able to expand laterally, even to a partial severance of the ventricles, the aortic arch shows its widest span, and the intervals between the innominata, the left carotid and the left brachial are longer.

Parsons in confirmation writes: "It would be quite easy, had I the space, to multiply examples showing the coincidence between a broad thorax and its outlet on the one hand, and separation of aortic branches on the other; these examples are so numerous that it seems justifiable to regard the arrangements as cause and effect."

No one, however, has shown which is the cause and which the effect. The arteries in their development precede the bony outlet of the chest, which very possibly conforms to their arrangement. And in man, with, so far as known, a uniform outlet, all the types have been found, though of that in Fig. 8 *A* only an imperfect example, the picture of which has been repeatedly copied (see Poynter's Fig. 37). In the bat, cited by Parsons as having a very wide thoracic outlet, there are but two trunks as in the "non-claviculate, narrow-chested" pig. Thus the interesting correlation between the diameter of the outlet and the number and spacing of the vessels passing through it, does not seem to account for the symmetrical and asymmetrical arrangements under discussion.

Returning to the hypothesis of symmetry as an end and aim of these designs, the relation of the arteries to the corresponding veins must be considered. For the veins, like the arteries, begin as symmetrical paired vessels, though totally different in their arrangement. Through ready and frequent anastomoses and atrophy of parts, they shift more freely than the arteries, and acquire a new symmetry quite closely conforming to that of the arterial system. As seen by comparing Figs. 9, 10 and 11, this conformity is most exact in the sheep (Fig. 9) and one wonders the more why the left subclavian artery has not traveled a half-inch higher to perfect the symmetry. In the pig (Fig. 10) the veins have made a pattern which would be much more closely followed by the arteries if the left subclavian artery should ascend the brachiocephalic. That further departure from the embryonic status has not as yet been effected, but is it unreasonable to suppose that in a geological

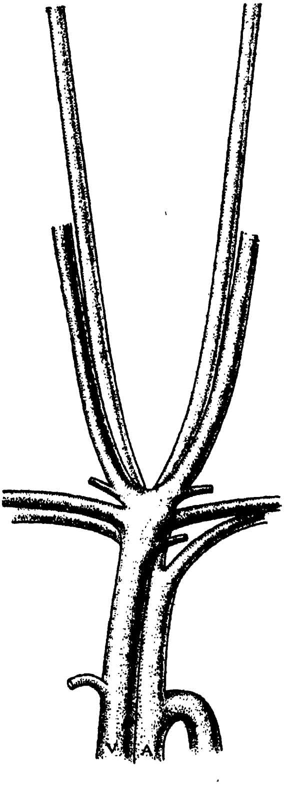

Fig 9

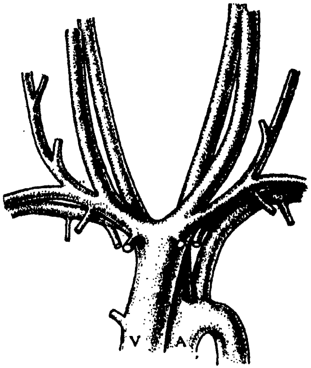

Fig. 10

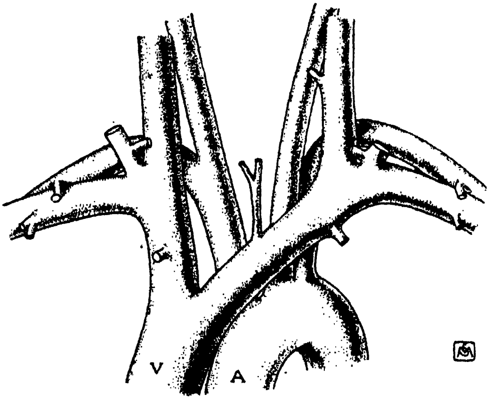

Fig. 11

FIGS. 9–11. The jugular and subclavian veins shown in relation with the carotid and subclavian arteries, together with the main trunks from which they proceed, and the beginnings of certain branches; *A*, arteries; *V*, veins. Fig. 9, the pattern of these vessels in the sheep; Fig. 10, in the pig; Fig. 11 (modified from Sobotta's Atlas), in man.

period it may be brought about? In man (Fig. 11) the distribution is still less perfect and two possibilities for symmetry are apparent. It would seem to be more readily attained by the formation of a left innominate vessel as happens in some anomalies; but the trend seems rather toward fusion of the left carotid with the innominate, thus starting upon the path already traversed in the pig and sheep. Whether or not either of these forms of symmetry may ever be attained is a question which we do not attempt to answer.

Having considered symmetry as a factor in the arrangement of these minor parts, something should perhaps be said concerning the disposition of the major viscera, where symmetry indeed seems to have lost control.

## THE DEXTRAL SPIRAL OF THE VISCERA

In the young mammalian embryo, bilateral symmetry prevails not only in the larger vessels, but in the heart itself, and in the digestive tube with all its appendages. For comparison with the later stage the diagrammatic ventral view, Fig. 12, may serve, though it is very far from resembling the actual appearance of any embryo. Above, the heart is shown as a median tube, bent so that its venous end is dorsal and its arterial end ventral. Below the diaphragm, an outline suggests the median position of the stomach, characteristic of its earliest stages. For a longer time the liver, in ventral aspect, is median and perfectly symmetrical, and below it, the gall-bladder is primarily in the midline. The ventral pancreas has symmetrical right and left lobes, which some regard as separate glands, and the dorsal pancreas at the outset is also bilaterally symmetrical.[20] The intestine forms a loop extending ventrally. Its upper limb is small intestine, which makes the bend and ends at the cæcum on the lower limb, the remainder of which is large intestine. Subsequently all these organs are involved in a dextral rotation, similar in direction to that of gastropod molluscs, producing the adult condition shown in Fig. 13. The cardiac loop and the intestinal loop, it will be noted, bend in precisely the same manner.

The dextral nature of the torsion of the primary loop of intestine as seen in Fig. 13 would become more evident if it were carried a half-turn further, as actually occurs in the pig. Such a condition is diagrammatically shown in Fig. 12 *c*, but has been very accurately drawn by Dr. Lineback in connection with his study of the remarkable spiral coil in the colon of the pig.[21] In the pig the colon forms a dextrally coiled mass of three or four complete revolutions, rarely winding sinistrally. The primary loop of intestine may also rotate sinistrally, but very rarely. If this primary loop should remain directed forward or ventrally, there would be but two possible arrangements in the adult, dextral and sinistral, respec-

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[20] These relations of the pancreas are further described in the *Amer. Journ. of Anat.*, 1911, Vol. 12, p. 389–400.

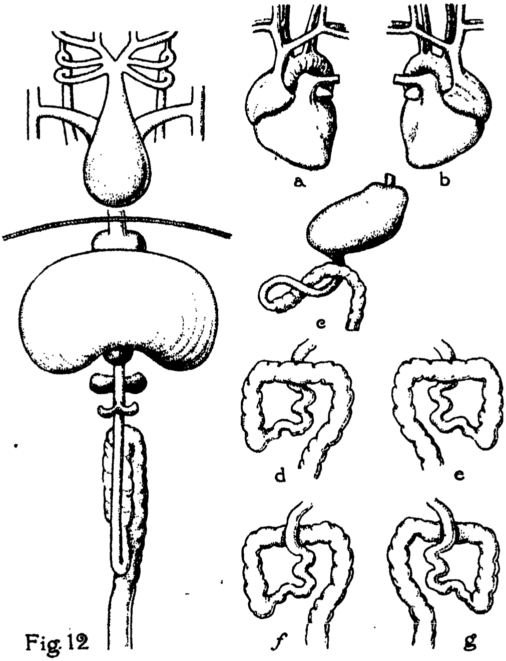

Fig. 12

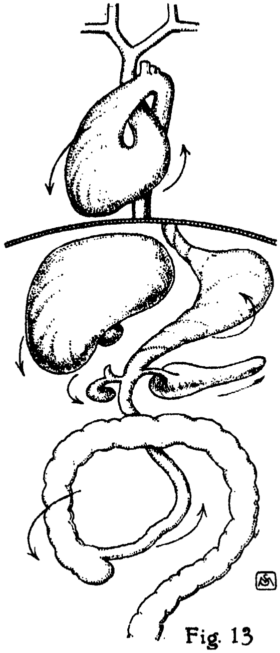
Fig. 13

Fig. 12. Diagram of the primitive bilaterally symmetrical disposition of the human viscera. Fig. 13, diagram of the adult arrangement resulting from a dextral rotation. Fig. 12. *a*, the normal heart and vessels; *b*, the same structures in situs inversus; *c*, diagram of the more extensive rotation of the primary loop of intestine as it occurs in the pig; *d*, the normal relation of the human colon and small intestine; *e*, their relatively frequent relation in situs inversus; *f*, retroposition of the colon in situs solitus, a very rare anomaly; *g*, retroposition in situs inversus, apparently never observed. It should be noted that *d* and *g* are dextrally rotated; *e* and *f*, sinistrally.

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[21] Lineback, P. E., "The Development of the Spiral Coil in the Large Intestine of the Pig," *Amer. Journ. Anat.*, 1916, Vol. 20, p. 483–503.

tively. But since the loop as a whole is deflected to one side or the other, so that the cæcum goes either to the right iliac fossa (situs solitus) or to the left (situs inversus), there are four possible arrangements. These are (1) the normal,—situs solitus with dextral torsion, Fig. 12 *d*; (2) situs inversus with sinistral torsion, Fig. 12 *e*; (3) situs solitus with sinistral torsion, known as retroposition of the colon, since the colon crosses the small intestine dorsally, Fig. 12 *f*; and (4) which has apparently never been observed, situs inversus with dextral torsion, likewise causing retroposition of the colon, Fig. 12 *g*. Although situs inversus, partial or complete, is relatively common, retroposition of the colon (Fig. 12 *f*) is quite rare. Tscherning in 1883 reported a case in a laborer of 56 years who died of intestinal obstruction, and since then several others have been recorded.[22]

The cardiac loop also rotates dextrally, with rare sinistral exceptions, but the rotation is by no means as simple a process as the diagrams imply. Essential details in the development of the cardiac loop in the cat have been recorded by Schulte, whose work has been reviewed and supplemented in Murray's careful study of the rabbit.[23] The dextral torsion has the appearance of being carried beyond the limits of the heart itself, by the atrophy of left veins and right arteries in the originally bilateral series. Cases of sinistral torsion of the heart (situs inversus, Fig. 12 *b*) may similarly be intensified by the degeneration of *right* veins and *left* arteries, completely reversing the normal picture. But there is also a group of anomalies, included among the cases known as "transposition," in which the veins and arteries degenerate as is normal, though the cardiac loop has reversed its bend. Remak observed and figured a reversed bend in the heart of a young chick embryo,[24] and, with the writer, Dr. Abbott made reconstructions to picture what would happen if hearts with such an initial anomaly should continue their development.[25] Lochte had previously ascribed cases of corrected transposition to "an inversion of the cardiac loop."[26] Uncorrected transposition, we believe, may be due to partial or imperfect rotation, either dextral or sinistral.

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[22] Tscherning, *Nordiskt med. Arkiv*, Bd. 15, No. 9, as cited with figures by Ekehorn, *Arch. f. klin. Chir.*, 1904, Bd. 72, p. 606. Strehl (*Arch. f. klin. Chir.*, 1908, Bd. 78, p. 13) presents an excellent figure of retroposition as found in a girl of 12 who died from the resulting obstruction. Cutore (*Anat. Anz.*, 1912, Bd. 40) in describing a case in an infant (figured on p. 385) refers (on p. 442) to previous records by Bastianelli (1904) and Righetti (1909). Hunter has recently recorded another case in an infant. *Brit. Med. Journ.*, 1922, II, p. 800–802.

[23] Schulte, *Amer. Journ. Anat.*, 1916, Vol. 20, p. 45–72. Murray, *ibid.*, 1919, Vol. 26, p. 29–39.

The dextral rotation of the other organs is simpler, since no loops are involved. The stomach has long been described as rotating so that its left surface becomes ventral and its right surface dorsal, the entire organ shifting from the median plane to the left. This, however, is a complex process of unequal growth rather than simple rotation. As the stomach goes to the left, the liver turns to the right. The pancreas rotates in such a way that the right lobe of the ventral pancreas pursues the dorsal pancreas around the intestine to fuse with it, and the left lobe of ventral pancreas, if it does not atrophy or remain in situ to form an annular pancreas, may grow out under the gall-bladder. The trachea and œsophagus share in the dextral rotation, as is strikingly shown by Dr. C. Chang of Hopei University in a study now in progress. Finally there may be mentioned the dextral spiral trend of the muscle fibers throughout the digestive tube.[27]

Various causes have been assigned for this dextral rotation. Sometimes it has been attributed to the veins.

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[24] Remak, R., "Untersuchungen über die Entwickelung der Wirbelthiere," 1851, Taf. III, Figs. 28, 29.

[25] This study has been only inadequately recorded—*Anat. Rec.*, 1915, Vol. 9, p. 103–105, together with brief references by Dr. Abbott in several publications.

[26] Lochte, "Ein Fall von Situs viscerum irregularis," *Beitr. z. path. Anat.*, 1898, Bd. 24, p. 187–222.

[27] Recently studied by Dr. Carey and Professor Sykes. *Cf. Science*, 1922, Vol. 55, p. 704–706.

"From our earlier investigations," wrote Lochte in 1898 (*l. c.*, p. 220–221), "we might assume that the normal position of the cardiac loop in situs solitus depended on the persistence of the left (*sic*) umbilical and omphalo-mesenteric veins." (The position of the stomach, duodenum and spleen he had likewise ascribed to the way in which the portal and umbilical veins develop.) "Without doubt in the normal formation of the cardiac loop these veins persist," he continues, "but it appears more than doubtful whether we are justified in recognizing a causal connection between the two: if one discards this hypothesis, the determining influence must reside in other factors which at present can not be more closely defined."

Three years after Lochte, the writer ventured the following opinion: "As the venous channels become predominant on the right side, the liver consequently develops more rapidly there and becomes a right-sided organ. Veins and liver combine to push the stomach to the left. . . . It may confidently be assumed that, had the originally symmetrical vessels persisted on the left side, stomach, liver, and later the vena cava would shift their position, resulting in situs inversus."

But these observations show merely the close correlation between the veins and the rotating organs, without locating the initiative—certainly it is not with the veins, predominant as they appear in sections. Papez in 1915, after a prolonged and careful embryological study, failed to find "a satisfactory mechanical explanation of intestinal rotation," but the influence of adjacent blood-vessels was considered eliminated. Rotation was ascribed to the growth of the epithelial tube. "The stomach swings boldly to the left and it appears that the intestine (*i.e.*, duodenum) is carried to the right by a compensatory bend of the elongating epithelial tube." "We are inclined to regard the gastric and intestinal bends together as forming an 'S,' comparable with S-shaped bends which soon develop in the mesentery itself."[28]

In what is perhaps the most recent study of "the mechanics of intestinal rotation," Vogt emphasizes the importance of this "alternating double coil" formed by the stomach and duodenum. The duodenum then turns back upon itself, pushing the mesentery to the left at the duodeno-jejunal flexure, and this flexure, according to

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[28] Papez, J. W., *Anat. Rec.*, 1916, Vol. 10, p. 220–221; 1917, Vol. 11, p. 392–394.

Vogt, is "the key to the understanding of intestinal rotation."[29] In discussing Vogt's paper before the *Anatomische Gesellschaft,* Braus expressed some doubt as to the efficacy of the duodeno-jejunal flexure. Vogt utilizes it for intestinal rotation only, which is independent of that of the stomach. In the left-sided position of the stomach he recognized "one of the primary asymmetries which must be regarded as predetermined."

It seems evident that the attempt to select any vessel or organ as the cause of the spiral rotation is ill-advised, since in some anomaly, almost every "cause" may be shown clearly to be inoperative. The true motive is more pervasive and deep-seated than any of its early manifestations. In the thoroughgoing inversion of symmetry in the gastropod molluscs, Conklin finds that the reversal is evident with the first cleavage of the egg, and thinks that it may proceed from a reversal of polarity in the oocyte.[30] In mammals the initial inversion must arise much later, after the organs have developed, with apparently an indifferent bilateral symmetry. But the primary direction of the polarity of the ovum and the secondary rotation of bilateral organs, both tend to produce a great predominance of dextral spirals, and their presumably common cause lies in a field other than morphology. Here we have sought merely to show that all the principal viscera in man are disposed in accordance with a general dextral rotation, like that which prevails in the gastropod molluscs.

## CONCLUSION

The examples which have been cited, inadequate as they may be, lead to the conclusion that nature is ill at ease—restless—in the presence of asymmetry. When a primary condition of symmetry has been lost, some new semblance of symmetry will be produced, and often a very perfect symmetry may be built upon the remains of that which has gone. Thus in plants we have seen that specific, generic, and even more far-reaching distinctions, may be evolved in this way. In mammals, a series of remarkable evolutionary changes, of little or no taxonomic value, have occurred in the aortic arches. If these are rightly interpreted on the basis of symmetry, further changes in the anatomy of man and mammals seem possible in a geological measure of time, and some seem so highly in accord with natural phenomena that the wonder is that they have not occurred already. Finally the spiral arrangement of the viscera in man, as superimposed upon, or derived from, bilateral symmetry, should be more comprehensively examined than heretofore, and must be reckoned with in connection with a wide range of anomalies, as well as in understanding normal anatomy.

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[29] Vogt, "Zur Morphologie und Mechanik der Darmdrehung," *Verh. d. anat. Gesel.,* 1920, p. 39–55.

[30] Conklin, E. G., "The Cause of Inverse Symmetry," *Anat. Anz.,* 1903, Bd. 23, p. 577–588.

*Postscript.* After the completion of this paper, Professor Conklin, in a notable course of Lowell Institute lectures, vigorously maintained that evolution must take place in the germ-cells, and especially in their chromosomes, to the exclusion of evolution in embryonic and later developmental stages, which it would be misleading to call "in the adult." It is difficult to see how this can be true of the floral variations and aortic patterns which have here been considered. That the future animal exists potentially and causally in the fertilized ovum seems proven by the subsequent course of events; yet to assume that the myriads of adult characters are there represented by particular genes or granules, through changes in which evolution is effected, implies a preformation far beyond the dreams of Hartsoeker and Dalenpatius, and subject to the same criticism which shattered them. A gene for so trivial a character as the iris-color should be accompanied by a hundred others for more important structural features of the eye, and thousands upon thousands, if all the bodily elements are similarly represented. The situation recalls Tyndall's train of thought when on the summit of the Matterhorn,—whether his pensiveness and the alpine peaks were potentially present in the earliest nebula!

From this incredible complexity we withdraw to a view in which epigenesis is recognized,—in which the body is not a by-product of the germ-plasm, and in which somatic changes play a large part in evolution. In the instance of the aortic arches, a somatic character, apparently acquired in embryos of some 10 mm., becomes an important feature in the evolution of various mammals. The now prevailing patterns in the pig and sheep, for example, presumably appeared in the ancestral animals as rare anomalies; these anomalies then became common; and finally, after they had become normal, these acquired characters could be called inherited. In the imporances here discussed, the cause of anomalies is the cause of evolution; and in these instances, typical of many others, it appears to be somatic rather than germinal.

# TWO NEW COLOR FACTORS OF THE GUINEA PIG

DR. SEWALL WRIGHT

BUREAU OF ANIMAL INDUSTRY, UNITED STATES DEPARTMENT OF AGRICULTURE, WASHINGTON, D. C.

THE common laboratory rodents, the mouse, rat, guinea pig, and rabbit, were among the first animals to be studied genetically, following the rediscovery of Mendel's law. Some half dozen more or less closely parallel pairs of Mendelian factors, affecting color, were soon discovered in each case. Work with these animals has continued, but new independent pairs of factors have not been coming to light very rapidly. Instead, a considerable number of new factors have been discovered which have turned out to be allelomorphs of those already known. We thus have 3 allelomorphs in the hooded series in rats, 4 in the albino series of guinea pigs and also of rabbits, and 3 each in the albino series of rats and mice. Of agouti series allelomorphs, 4 are known in mice, 3 in rabbits and 3 in guinea pigs. There are 3 allelomorphs affecting density of black in rabbits and 3 in the tortoise-shell series of guinea pigs.[1]

One of the new factors of the guinea pig to be discussed here is of this kind, a fifth member of the albino series. The other has no known counterpart among rodents. Its closest parallel seems to be in certain imperfectly understood color variations among hogs.

The highest dominant (C) in the albino series of guinea pigs (Wright, 1915, 1916) is present in the ordinary intensely colored varieties showing black or red or both in the fur. Below this in dominance and order of effect is a grade of dilution of color ($c^d$) in which black is reduced to a sepia color and red to yellow or cream. The eyes remain black. In the red-eyed dilutes with the next allelomorph ($c^r$) black is still represented by a sepia, darker even than in the previous case, but all red is eliminated from the coat. The red areas of tortoise shells and golden agoutis are replaced by white, giving us black and white guinea pigs with the tortoise shell instead of the piebald type of pattern, and silver agoutis. There is reason to believe that the intensification of sepia with $c^r$ as compared with that found with $c^d$ is due to the release of black pigment production from competition for some common element with the yellow-producing process (Wright, 1916–1917). Albinism ($c^a$) is the lowest member of the series. In guinea pigs complete albinism is not known except as the result of combinations of several factors which reduce pigment. The so-called guinea pig albinos have dark noses, ears and feet, and often sootiness on the back. As in the case of $c^r$, some black pigment is produced, but no yellow. The eyes are pink.

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[1] A discussion of these multiple allelomorphic series with references to the original publications was given in a series of papers by the writer "Color Inheritance in Mammals," *Jour. Her.*, 8, 9, 1917, 1918. Since that time Castle (1921) has added a fourth member to the albino series of rabbits and Detlefsen (1921) has added a third to the albino series of mice. Other less clearly established cases have been suggested.

The intensity factor, C, is completely dominant over the others. Below this there is imperfect dominance. Where the homozygous dilutes $c^dc^d$ have medium sepia and yellow, the heterozygotes $c^dc^r$ and $c^dc^a$ have dark sepia and cream, and light sepia and cream, respectively. The homozygote $c^rc^r$ is almost black and white with very dark-red eyes, while $c^rc^a$ is a light or medium sepia with light-red eyes.

On commencing investigation of the stocks of guinea pigs which had been maintained by the Bureau of Animal Industry, the writer found that intense types, dark-eyed dilutes, and albinos of the ordinary sooty kind were present. There were no red-eyed dilutes. All red-eyed dilutes in this country, probably, trace to a few animals brought from Peru in 1912 by Professor Castle (Castle, 1916). There were several inbred families which had been maintained by brother-sister mating since 1906, which the records indicated to be homozygous intense in all lines living in 1916 (Families 2, 24, 31, 32, 34, 38 and 39). Others were found to be homozygous dilute in all lines at that time (14, 35 and 36). Both intense and dilute lines were present in three families (18, 20 and 23) and both intense and albino lines, or segregates, in three more (7, 13, and 17). One family (9) was predominantly dilute, but there were albino segregates.

Crosses soon made it clear that the dilution present in these families was allelomorphic with albinism, as in the case of that previously encountered by the writer in Professsor Castle's laboratory. Minor variations in intensity were found, however, which were not in the albino series. Family 32, for example, was characterized by a very intense red, family 38 by a light red, approaching yellow. The lines in family 18 which were not permanently intense red produced young much like family 38 at birth, but which became typical yellow later. Families 35 and 36 produced only young of a typical yellow. Crosses with albinos reduced the intensity of the red of family 32, but raised that of family 38. On the other hand, the yellow of both families 18 and 35 was reduced to the cream characteristic of dilutes heterozygous for albinism. It was thus clear that the marked difference in intensity between families 32 and 38 was not due to an albino series allelomorph. Both have factor C. Multiple independent modifying factors seem to be responsible for the difference in this and other cases of this kind. The first cross is intermediate, as is also $F_2$. No recognizable segregation has been observed. Similarly, the same dilution factor of the albino series seems to have been present in families 18 and 35 and all of the other dilute inbred families. We will not be concerned further in this paper with these minor variations in intensity, brought to light by inbreeding and lost on crossing.

While the dilutes of the inbred families were found to possess an allelomorph of albinism, there was a difference in appearance from the dilutes with which the writer had been familiar. There was much less dilution of the black parts of the fur. The black in the homozygous dilutes was almost indistinguishable from that of intense guinea pigs, and those heterozygous for albinism were of a dark sepia color, never approaching the light sepia characteristic of Professor Castle's stock. On the other hand, the dilution of red (yellow in homozygous dilutes, cream in heterozygotes) was not conspicuously different from that in the latter stock.

This difference in color was made more evident by comparison with some dilutes which were kindly presented by Professor Castle. Knowing, however, that Professor Castle had especially selected for extreme dilution for several years (Castle, 1912) it was thought that the difference would probably turn out to be due to modifiers, as in his selection experiment with hooded rats (Castle, 1919). No special study of the variations in dilution was made at this time, but crosses were made with Professor Castle's dilutes for another purpose. During the course of the next two or three years it was noticed that typical light sepias occasionally segregated out among the descendants of these crosses. Experiments were then begun, to determine whether the difference was transmitted independently of albinism or not.

Light sepias, tracing to Professor Castle's dilute selection stock were mated with albinos of the Bureau stock, while dark sepias whose dilution factor came from families 9, 18 or 35 were mated with albino sons or daughters of light sepias. In the next and later generations, the dilutes from each type of mating were mated with albinos from the other.

If the difference in intensity were due to factors independent of the albino series, as suspected at first, it should be transmissible through albinos and the sepias from the two types of mating should be indistinguishable. In later generations, both dark and light sepias should segregate out of both if they did not merely blend together like the intense and light reds of families 32 and 38, previously discussed.

As it has turned, however, the two series have kept wholly distinct. The dark sepia of the Bureau line is as dark as ever and the light sepia tracing to Professor Castle's stock is as light as ever after as thorough a mixing of blood lines for several generations as is possible, through the albino parents. All young have been graded by standard sets of skins, the sepia set running from grade 3 for the lightest sepia to 14 for intense black and the yellow set running from grade 3 for the lightest cream to grade 13 for the red of family 32. The average grade in the dark series has been sepia 11.5, cream 4.6; in the light series, sepia 6.9 and cream 4.2. The lower limit of sepia in the dark series has been an occasional grade 10 and the upper limit in the light series a rare grade 9.

This result made it practically certain that a new allelomorph of albinism was involved. The symbol $c^k$ has been adopted for this factor. The two types of mating may be represented as follows:

| | Dark dilute | Light dilute | Albino |
|---|---|---|---|
| (1) $c^dc^a \times c^ac^a$ (from 2) $= c^dc^a + c^ac^a$ | 0 | 81 | 98 |
| (2) $c^kc^a \times c^ac^a$ (from 1) $= c^kc^a + c^ac^a$ | 64 | 0 | 48 |

The existence of the new factor has been verified by production of all of the new compounds, $c^kc^k$, $c^kc^d$, $c^kc^r$, and $c^kc^a$, all thoroughly tested by matings with albinos and otherwise. The results have all been in conformity with the hypothesis, both qualitatively and quantitatively within the limits of random sampling.

All of these combinations have black eyes, as of course was to be expected. The homozygous dark dilutes $c^kc^k$ have a very dark sepia, difficult to distinguish from blacks in some cases even by direct comparison, but a yellow averaging only slightly more intense than that of $c^dc^d$. The heterozygote between the two dilution factors, $c^kc^d$, is intermediate in color—a dark sepia and a typical yellow. The type $c^kc^r$ is almost intense black, but with a typical cream, a striking combination. The heterozygotes with albinism $c^kc^a$ are as described above, dark sepia and cream. The five intense types, CC, $Cc^k$, $Cc^d$, $Cc^r$ and $Cc^a$, have all been produced and tested. They are indistinguishable in appearance. Among the remaining 10 types, all are ordinarily distinguishable from each other if both sepia and yellow are present in the fur, except, curiously enough, the compounds $c^kc^a$ and $c^dc^r$, which have no factor in common.

After finding this new member of the albino series, dilutes from all sources in the Bureau stock were tested for a possible sixth allelomorph. Yellows approaching red, and creams approaching yellow were found as well as some rather aberrant sepias. On mating with albinos from matings 1 and 2 above, these minor differences promptly disappeared in all but one case. With this one exception, all of these dilutes proved to have factor $c^k$ or an allelomorph so close as to be indistinguishable. The exceptional case was from a mating (B211) in the random bred control stock, between an albino male and an intense golden agouti tricolor female. This control stock is the stock from which the various inbred families were wholly or in part derived and has been maintained with the careful avoidance of inbreeding. Little study had previously been made of its colors which had seemed to include nothing unusual. The above mating (B211) produced black-yellow and yellow agouti tricolors in addition to the ordinary intense black-red and golden agouti varieties. It seemed most likely that it was of the type $Cc^k \times c^ac^a$, but the dilute young showed a typical yellow (grade 7 or 8) in place of the cream (grade 4 or 5) usually found in $c^kc^a$, and a black of full intensity (grade 14) in place of dark sepia (grade 11 or 12). There were 11 young with red in the fur and 5 with yellow, in addition to an unclassifiable black—white bicolor. A mating between two of the dilute young produced six dilutes of their own type in addition to two albinos.

A dilute son and a dilute daughter of the original mating (B211) were mated with albinos from a type 1 mating in order to test for the suspected presence of a sixth allelomorph. According to all past experience there should only have been dilute and albino young. The result, however, was 5 young with red in the fur, 5 intense blacks showing no red or yellow, and 17 albinos. A similar result was obtained from two dilutes from the mating between dilute progeny of B211 referred to above. These were mated with albinos of the ordinary stock and produced 9 intense young with red in the fur and 5 albinos, both happening to transmit the albino factor. These four matings of dilute by albino thus produced 20 intense young (14 showing intense red as well as intense black) in addition to 22 albinos.

This intensity must apparently have come from the albino parents in each case, since the new dilution was clearly recessive to the intensity of its own stock. An intensity factor transmitted by an albino could clearly not be the intensity factor (C) of the albino series. The symbol f has been adopted for the new dilution factor, and F for its dominant allelomorph.

The original mating, B211, was probably $CCFf \times c^ac^aFf$ (11 intense; 5 dilute young). The matings of dilute progeny with ordinary albinos were of type $Cc^aff \times c^ac^aFF$, giving intense young $Cc^aFf$ in addition to albinos $c^ac^aFf$.

Some of the intense young were back crossed to albinos of ordinary dilute stock. No dilute young appeared. There were 16 intense (8 showing red, 8 merely intense black) and 18 albinos. This, of course, is in harmony with the above hypothesis.

On the other hand, on crossing the $F_1$ young with their albino brothers or sisters, at least one dilute segregate of the new type was produced. These matings have produced 10 young showing red, 1 with yellow and 5 blacks, which could not, of course, be classified relative to the new dilution, and 14 albinos. A mating between two $F_1$ intense young, which should produce similar results, except for the proportion of albinos, has produced 1 young with red, 1 with yellow and 1 unclassifiable black.

Excluding the albinos and unclassifiable blacks, we have an $F_2$ ratio of 11 black-red intense to 2 black-yellow dilutes. As there is no intergrading of the red and yellow, there can be little doubt that a single recessive factor is involved.

Attempts have recently been made to combine this new dilution with that of the albino series. A mating between the two types ($Cc^aff \times c^kc^kFF$) resulted in 6 young with red ($Cc^kFf$) and 3 dark sepia-cream dilutes ($c^kc^aFf$).

Three matings between albinos known from their parentage to transmit the new dilution ($c^ac^aFf$) and ordinary dilutes ($c^dc^aFF$, $c^kc^kFF$) have resulted in 14 young like ordinary light or dark dilutes in appearance. The new black-yellow dilution was recovered in the next generation in the same litters as ordinary dilutes of the sepia-cream or sepia-yellow types.

One very interesting young one was produced by a mating known from the parentage of the dam and sire to be of the type $Cc^aFf \times Cc^dFf$. Among the young were a black-red ($C—F—$), a black-yellow ($C—ff$), a light sepia ($c^dc^aF—$) and a dark sepia-cream, several grades darker in its sepia (grade 13) than any heterozygous dilute of type $c^dc^a$ ever graded before. A similar dark sepia has come from the mating $Cc^aff \times c^dc^aFf$. These anomalous dark sepias must apparently represent the desired combination of dilution factors $c^dc^aff$. If this is confirmed by the tests in progress it indicates that the new dilution factor intensifies black while diluting red. If we assume that its primary effect is the dilution of red the intensification of black can be explained as due to the partial release of the black producing process from competition with the process for producing red. The situation is somewhat comparable to the relation between factors $c^d$ and $c^r$ in the albino series, already referred to.

Animals with the new dilution factor have a typical yellow color when born. Later in life this changes to cream and in some cases, at least, it ultimately fades out altogether, leaving white. This is another contrast with the effects of the dilution factors of the albino series. The yellows ($c^kc^k$, $c^kc^d$, $c^dc^d$) and the creams ($c^kc^r$, $c^kc^a$, $c^dc^r$, $c^dc^a$) have not been observed to change in intensity with the exception of the relatively slight change previously referred to in family 18. The black of the new dilutes remains intense. There is a gradual intensification of sepia in the dilutes of the albino series.

No factor with an effect of this kind has been described hitherto in rodents. No provision for it was made in the scheme for classification of mammalian color factors suggested by the writer in previous papers (Wright, 1916, 1917a). Certain color variations of the hog were, however, interpreted as due to dilution of red without any apparent dilution of black (Wright, 1918). A dominant factor of this kind seems to be present in Yorkshires (white) and Chester Whites in addition to a dominant factor which greatly restricts or eliminates black in the skin and bristles. It was also suggested that the black with white points of Berkshires and Poland Chinas represents a tortoise shell pattern of black and red (instead of piebald black and white as in Hampshires) in which red has been eliminated by specific dilution factors. This interpretation of the Berkshire and Poland China patterns has been confirmed in recent experiments by Detlefsen and Carmichael (Detlefsen and Carmichael, 1921).

It will thus be necessary to add a new class of color factors, specific diluters of red color, which will probably in general be found to have an intensifying effect on black.

## SUMMARY

A fifth member of the albino series of guinea pigs, dark dilution, $c^k$, has been identified. It causes distinctly less dilution of black pigment than does the previously known dilution factor $c^d$, although very little less dilution of red. It is recessive to intensity (C) but imperfectly dominant over light dilution ($c^d$), red eyed, non-yellow dilution ($c^r$) and albinism ($c^a$). The allelomorphic series, C, $c^k$, $c^d$, $c^r$, $c^a$, is the longest yet reported in mammals.

A factor (f) reducing red to a yellow, which fades later to cream and even white, but intensifying black, has been found among the descendants of a single mating. It behaves as a unit recessive to its normal allelomorph (F) and is transmitted independently of the albino series.

It is suggested that the intensification of black is a secondary consequence of a primary dilution of red and is due to a partial release from a competition between the processes of black and red color production, and is thus parallel to certain effects, previously described in the albino series.

This factor represents a new class of color factors in rodents. Its closest parallels seem to be found in certain color varieties of the hog.

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# INHERITANCE IN DROSOPHILA HYDEI. I. WHITE AND VERMILION EYE-COLORS

DR. ROY E. CLAUSEN

UNIVERSITY OF CALIFORNIA

In August, 1920, I collected locally a number of wild species of Drosophila, among them a large species with a spotted thorax which Doctor A. H. Sturtevant later identified for me as *hydei* (for a description of the species cf. Sturtevant, 1921). Stock cultures of the species were easily established and maintained in the usual way. The species was grown rather extensively and the cultures were examined closely for aberrant individuals. A number were found from time to time, but most of them failed to transmit their characteristics. Most of the deviations from type affected the wings, which are so frequently subject to somatic variations that the failure to establish them is not surprising.

One form which appeared in the stock cultures in September, 1920, proved to be a new genetic type. It is a form similar in appearance to "bobbed" in *melanogaster*. The dorso-central and scutellar bristles are reduced in size, and the markings on the abdomen may be either normal or of the scaly, irregularly-marked appearance which is exhibited by "bobbed" in *melanogaster*. The character is sex-limited, expressed only in females, and it reduces viability somewhat. Its mode of inheritance has not been determined. An attempt was made to establish a pure race by selection, but thus far it has not succeeded or the character is highly variable in expression. It is mentioned here because most of our stocks of *hydei* contained it at the time the experiments reported in this paper were performed, and its presence accounts for the discrepancies in the sex ratios exhibited by some cultures. Our locally-derived wild-type stock continually produces it, and our "bobbed" stocks still produce some wild-type individuals. One wild-type stock, however, which we received from Doctor Sturtevant, a stock collected in the summer of 1920 in Alabama, is free from it. This stock has been carried under the designation, Stt.

## White Eye-color

On March 9, 1922, a single white-eyed male was discovered in the wild-type stock. The eye-color of this male was pure white, identical in appearance with the corresponding character in *melanogaster*. No other white-eyed flies were discovered subsequently in the stock, although a number of females were tested separately to determine whether or not they were heterozygous for it.

The white-eyed male was mated to two females from the same stock, producing in culture no. 1, 178 wild-type females and 204 wild-type males. The same male was then mated to a female from the Stt stock, producing in culture no. 8, 121 females and 138 males, all wild-type. He was subsequently mated in culture no. 14 to four of his daughters from culture no. 1. Culture no. 14 produced 27 wild-type females, 57 wild-type males, 18 white females, and 69 white males. He was then mated in culture no. 29 to a wild-type daughter from culture no. 8. In culture no. 29 five sub-cultures were made at seven-day intervals, and these produced 151 wild-type females, 354 wild-type males, 129 white females and 298 white males. He was taken from culture no. 29 and mated in culture no. 97 to a wild-type female from culture no. 29. There were three sub-cultures under this culture number, which yielded 71 wild-type females, 195 wild-type males, 77 white females, and 223 white males. The complete history of the original white-eyed male has not yet been told. From culture no. 97 he was transferred with one of his daughters from the same culture to culture no. 111. This culture produced no flies. He was accidentally killed on June 7th while transferring him from one bottle to another. He lived 90 days in an incubator room maintained at 25° C. We have since found that this is not an unusual duration of life for males of this species.

White eye-color, symbol *w*, is clearly a recessive sex-linked character which exhibits exactly the same mode of inheritance as white eye-color in *melanogaster*. Various matings of white with wild-type have been made many times and have always been found to agree with expectation save for discrepancies in the sex ratio, due apparently to the presence of "bobbed," which reduces viability. These results are so elementary that it is not thought worth while to present the actual experimental data.

The white character exhibits no significant effect on viability. White flies of both sexes are fully fertile. In this respect they resemble white in *melanogaster* and differ from white in *obscura*, the females of which are reported by Lancefield (1922) to be sterile. Stocks of white have been established and maintained without any difficulty. A stock free from "bobbed" has been produced by repeated out-crossing to the Stt stock.

## VERMILION EYE-COLOR

On March 29, 1922, an examination of the "bobbed" stock revealed the presence of seven males with a bright vermilion eye-color. Subsequently another bottle also produced vermilion segregants. Counts were made of the flies which emerged in this latter bottle. It produced 178 wild-type females and males and 34 vermilion males. The results probably indicate that one of the female parents of this stock culture was heterozygous for vermilion.

A number of matings were made of vermilion males with wild-type females from the same bottle. Of these only one, culture no. 22, produced anything but wild-type flies. It produced 35 wild-type females, 28 wild-type males, 34 vermilion females and 47 vermilion males. From this culture it was possible to establish a stock of vermilion flies, which, however, also exhibited the "bobbed" character.

Vermilion eye-color, symbol *v*, is, like white, a character of the first rank for genetic studies. The color is almost exactly the same as that of vermilion in *melanogaster*. Since the wild-type eye-color of *hydei* is distinctly darker than that of *melanogaster*, the difference between vermilion and wild-type in the former is more marked than it is in the latter. In vermilion the ocelli are almost white, as they are in vermilion *melanogaster*, but they are not as distinctly white as those of white-eyed flies. Vermilion is a recessive sex-linked character which gives the usual results when crossed with wild-type. Numerous cultures have been counted of all matings of this type without observing a single deviation from expectation.

## LINKAGE OF WHITE AND VERMILION

Since white and vermilion are both sex-linked, they should, of course, exhibit linkage with each other. Moreover, since the characters are sex-linked, it is possible to secure linkage data without first establishing a double recessive race of white-vermilion flies. As a starting point, a white female was mated to a vermilion male. The $F_1$ progeny consisted of wild-type females and white males. In order to secure linkage data, $F_1$ wild-type females were mated singly to vermilion males. Any kind of male would have served the purpose of this test, but vermilion was chosen because of a desire to establish eventually a white-vermilion race. The results of the cultures are recorded in section A, Table I.

In order to obtain white-vermilion flies, a number of vermilion females from culture no. 85 were isolated and mated singly to white males. All of these cultures except one produced only wild-type females and vermilion males. The exception, culture no. 101, produced 70 wild-type females, 69 white females, 58 vermilion males and 61 white males. White-vermilion is indistinguishable from white, but the white males produced in this culture obviously must have been white-vermilion in composition. These white-vermilion males mated to wild-type females from the Stt stock produced wild-type females and males.

$F_1$ wild-type females from these cultures were mated singly with vermilion males in order to obtain recombination data. The results are recorded in section B, Table I.

TABLE I

Section A, $P_1$, white ♀ × vermilion ♂; BC, $F_1$ wild-type ♀♀ × vermilion ♂♂, singly. Section B, $P_1$, wild-type ♀ × white-vermilion ♂; BC, $F_1$ wild-type ♀♀ × vermilion ♂♂, singly.

| Section A | Females | | Males | | | Section B | Females | | Males | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | + | v | v | w | + | | + | v | + | w | v |
| 85 | 64 | 84 | 84 | 82 | 7 | 143 | 111 | 98 | 85 | 106 | 12 |
| 86 | 58 | 63 | 41 | 63 | 5 | 144 | 91 | 84 | 114 | 101 | 5 |
| 87 | 100 | 74 | 66 | 75 | 6 | 145 | 100 | 100 | 93 | 96 | 11 |
| 88 | 63 | 55 | 51 | 59 | 2 | 146 | 74 | 69 | 83 | 86 | 13 |
| 89 | 94 | 95 | 84 | 84 | 4 | 147 | 75 | 74 | 73 | 79 | 9 |
| 90 | 64 | 73 | 60 | 77 | 9 | 148 | 64 | 57 | 67 | 66 | 10 |
| 92 | 82 | 79 | 57 | 96 | 9 | 149 | 77 | 62 | 58 | 45 | 11 |
| 93 | 53 | 61 | 71 | 66 | 6 | 150 | 48 | 43 | 34 | 47 | 2 |
| 94 | 140 | 129 | 117 | 133 | 9 | 151 | 80 | 87 | 80 | 83 | 15 |
| 95 | 10 | 7 | 11 | 7 | 2 | 152 | 87 | 90 | 105 | 95 | 14 |
| Total | 728 | 720 | 642 | 742 | 59 | | 807 | 764 | 792 | 804 | 102 |

In the determination of the percentage of recombinations from these data allowance must be made for our inability to separate white from white-vermilion. The simplest way to do this to multiply the visible recombination class, wild-type males in section A, and vermilion males in section B by two and divide by the total number of males. The females in these cultures obviously furnish no data on recombination. Applying this method to the data of section A, the recombination value from $\frac{w}{v}$ females is 8.2 per cent., and in section B from $\frac{w\ v}{}$ females, 12.0 per cent. The average value obtained by lumping the data together is 10.3 per cent. of recombinations.

The data may, however, be subjected to another form of treatment based on the inclusion in the white class of section A of white, parental, and white-vermilion, recombination, sub-classes; and in white of section B of the same sub-classes with reversed significances. If we make use of the entire data and calculate the recombination percentages by application of the method of least squares, we obtain for section A, 10.0 per cent.; for section B, 8.6 per cent.; and for the totals from both sections, 9.3 per cent. of recombinations.

## DISCUSSION OF RESULTS

White and vermilion in *hydei* to all appearances correspond to the characters of the same names in *melanogaster*. It is, however, impossible to apply the direct test of crossing to demonstrate a parallelism between them because the two species will not hybridize. The recombination percentage of white and vermilion in *hydei,* 9.3 per cent., is distinctly lower than that reported by Morgan and Bridges (1916) for the corresponding loci in *melanogaster,* 30.5 per cent.; but it does agree closely with the map distance between white and vermilion in *obscura,* reported to be 8 units by Lancefield (1922), and that between yellow and vermilion in *virilis,* reported by the same author from data secured from Metz to be about 14 units. It is, of course, impossible to decide as yet what these differences signify, but their existence demonstrates the importance of pursuing parallel genetic studies among the various species of Drosophila.

Besides the characters described in this paper, Hyde, for whom the species was named, has discovered and studied two others: scarlet (1915) and an eye-character, called variable (1922). These two characters are both recessive autosomal characters. Hyde's (1922) data indicate that they belong to the same linkage group and exhibit about 25 per cent. of crossing-over. Sturtevant (1921) lists *hydei* as a species possessing a chromosome complex of type I of Metz (1916); *i.e.,* five large pairs of chromosomes of approximately equal size and one small pair. Six linkage groups, therefore, are to be expected, of which two have been demonstrated.

The possession of two excellent sex-linked characters paves the way for studies of non-disjunction in *hydei.*

We have not yet been able to establish a non-disjunction stock in the species, although numerous attempts have been made to secure exceptional individuals from crosses of wild-type with vermilion and white, and of vermilion with white. In one culture, no. 98, of wild-type ♀ with white ♂ a single exceptional white male was secured among 596 flies. He was successively mated to three females during the 76 days he lived; and sub-cultures were established at 7-day intervals during this period in order to provide the best possible conditions for the production of offspring. None of the matings, however, yielded any progeny. Apparently this male was an XO individual produced by primary non-disjunction in the female. If so, XO males in *hydei* are sterile, like those in *melanogaster*.

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# A RED-SPOTTED SEX-LIMITED MUTATION IN BRUCHUS[1]

DR. J. K. BREITENBECHER

UNIVERSITY OF OKLAHOMA

IN the wild type of *Bruchus quadrimaculatus* which we have in our laboratory, the body color of both male and female is tan. This tan color the writer (1921)[2] described for it and its mutants (red, black and white) as belonging to the red (R) allelomorph body color series. Each mutant character is sex limited to a marked degree because every male for each mutant culture has tan elytra and body color instead of red, black or white elytra and body color, as their respective females have.

This paper concerns another sex-limited trait which is likewise somatically visible in the females but not in the males. In addition to the tan body color, the wild type of female has four black spots on her elytra, two on each elytrum, but the wild male has no spots on his elytra. This dimorphism is unique. On Sept. 22, 1921, the writer discovered in a culture pure for red (RR) a female having four red spots on her elytra instead of the usual four black spots. This female mutant was mated with a male from the same red culture from which she originated to determine if this new trait would breed true. Her progeny consisted of red spotted females and non-spotted males.

After several generations of selective breeding by mating virgin red-spotted females with males from this same stock, a culture pure for this trait was obtained. But as in the preceding case, there is complete dimorphism, for homozygous males have no red spots nor any spots at all. One can not easily distinguish externally the males of the black-spotted cultures from the non-spotted males of the red-spotted homozygous stock. This relation is a sex-limited one because of two types of females and one kind of male. This is different from any other work reported as far as the writer is aware. We have records of sex-limited conditions where one type of male at least is similar to one of the female types or the converse. But in *Bruchus* the males carrying these genes are non-spotted, a condition not appearing in females.

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[1] Contribution from the Zoological Laboratory of the University of Oklahoma Second Series No. 29.

[2] Breitenbecher, J. K., 1921, "The Genetic Evidence of a Multiple Allelomorph (Triple) System in Bruchus and its Relation to Sex-Limited Inheritance, *Genetics*, Vol. 6: 55–90.

## THE BREEDING TESTS

By making a few preliminary tests it was discovered that the gene, red spots, is a complete dominant to black spots. The writer, therefore, used the symbols SS to designate red spots, and ss for the black ones. It was further discovered that these two contrasting characters were easier to distinguish in a culture pure for red body color (RRSS) carrying red spots and the second culture homozygous for red body (RRss) and black spots. An insect (RRSS) pure for red body and red spots showed upon examination that both were of the same degree of redness; however, these red spots were transferred to other factors of the R allelomorphs, so that red body and red spots are not caused by one factor, but by two which make an insect appear pure red except where the pattern in the female outlines the red spots. The same relation was again found for a black body color, and black spots ($R_bR_bss$) in the same individual are not determined by one gene but by two separate ones; even though the amount of pigment is often of the same degree. Cultures were also made pure for white bodies and black spots ($R_wR_wrr$). The wild stocks are always homozygous for tan bodies and black spots (rrss). The males, however, from any culture are always like the wild phenotype (tan, non-spotted).

Whenever a homozygous, red spotted (SS) female is mated with a wild-type male, pure for black spots (ss), all progeny appear as red-spotted (Ss) females and wild-type (Ss) males. The $F_1$ offspring manifest a 1:1 sex-limited ratio, because the red spots in the males do not show, for the males never show spotting. The progeny from five such pairs are tabulated in Table I.

## TABLE I

$P_1$ A Homozygous Red-spotted Female (SS) × A Wild-type Male Homozygous for black spots (ss)
$F_1$ as follows:

| Pedigree Number of Each $P_1$ Pair | Females, Red Spotted (Ss) | Males, Wild Type[3] (Ss) |
|---|---|---|
| 103 | 18 | 14 |
| 109 | 81 | 82 |
| 110 | 25 | 29 |
| 111 | 42 | 38 |
| 115 | 15 | 21 |
| Totals | 181 | 184 |
| Calculated | 182.5 | 182.5 |

## TABLE II

### Reciprocal Cross

$P_1$ 1 Black-spotted Female (ss), × 1 Wild-type Male (SS)
$F_1$ as follows:

| Pedigree Number of Each $P_1$ Pair | Females Red Spotted (Ss) | Males Wild Type (Ss) |
|---|---|---|
| 101 | 27 | 29 |
| 104 | 25 | 23 |
| 106 | 32 | 33 |
| 113 | 33 | 25 |
| 114 | 36 | 46 |
| Totals | 153 | 156 |
| Calculated | 154.5 | 154.5 |

The reciprocal cross with its data are collected in Table II. In this cross the female was homozygous for black spots (ss) and the wild-type male was pure for red spots (SS). The progeny from the five pairs mated gave females which were red spotted (Ss) and males of the wild non-spotted type, which were also actually heterozygous (Ss) for red spots. A 1:1 sex-limited ratio again appears as a result of this condition.

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[3] Whenever the "Wild-type Male" is mentioned, it means that every male manifests a non-spotted phenotype for the pure cultures of the dominant factor, red spots, and its recessive allelomorph, black spots, and also for their hybrids.

The results of both crosses demonstrate that the red spotted factor is a complete dominant to black spots. These allelomorphs are manifested both phenotypically and genotypically in the females, but only the latter in the males. It is evident that the $F_1$ progeny from both tests were heterozygous and consisted of all red-spotted (Ss) females and wild-type (Ss) males. Likewise when these pairs were mated their $F_2$ offspring, as tabulated in Table III, follow a 3:1:4 sex-limited ratio. The results of the seventeen pairs mated prove that there are three times as many red-spotted (SS, Ss, sS) as black-spotted (ss) females, and further that there are actually four (SS, Ss, sS, ss) possible combinations for the males, although they appear as one phenotype.

TABLE III

$F_1$ 1 Red-spotted Female (Ss), × 1 Wild-type Male (Ss)
$F_2$ as follows:

| Pedigree Number of Each $F_1$ Pair | Females | | Males |
|---|---|---|---|
| | Red Spotted (SS, Ss, sS) | Black Spotted | Wild Type (SS, Ss, sS, ss) |
| 111.1 | 29 | 10 | 24 |
| 111.2 | 23 | 10 | 33 |
| 111.3 | 29 | 9 | 49 |
| 111.5 | 22 | 5 | 40 |
| 113.1 | 23 | 7 | 31 |
| 113.2 | 35 | 10 | 64 |
| 113.8 | 17 | 5 | 39 |
| 113.10 | 24 | 8 | 35 |
| 114.1 | 46 | 16 | 77 |
| 114.2 | 30 | 8 | 29 |
| 114.4 | 35 | 9 | 37 |
| 114.5 | 29 | 10 | 36 |
| 114.6 | 22 | 8 | 22 |
| 114.7 | 18 | 7 | 23 |
| 115.1 | 32 | 10 | 41 |
| 115.2 | 45 | 14 | 73 |
| 115.3 | 10 | 7 | 19 |
| Totals | 468 | 153 | 642 |
| Calculated | *459* | *153* | *612* |

The next procedure consisted in carrying out the usual back cross tests. The first one consisted in mating a $F_1$ red-spotted (Ss) female with a wild-type male, pure for black (ss) spots. The progeny from five pairs, shown in Table IV, consisted of red-spotted (Ss) females, black-spotted (ss) females, and wild-type (Ss, ss) males. These phenotypes manifested a 1:1:2 sex-limited ratio. Of the two kinds of males, however, half were actually heterozygous for red spots and black ones and half homozygous for black spots.

### TABLE IV

### BACK CROSS TEST

$P_1$ 1 Red-spotted Female (Ss), × 1 Wild-type Male (ss)
$F_1$ as follows:

| Pedigree Number of the $P_1$ Pair | Females | | Males Wild Type (Ss, ss) |
|---|---|---|---|
| | Red Spotted (Ss) | Black Spotted (ss) | |
| 101.1 | 16 | 19 | 36 |
| 101.2 | 19 | 16 | 31 |
| 109.8 | 13 | 11 | 29 |
| 109.9 | 5 | 3 | 8 |
| 109.11 | 15 | 18 | 34 |
| Totals | 68 | 67 | 138 |
| Calculated | *68* | *68* | *132* |

The second back cross test was the reciprocal of the previous one. The female was homozygous for black spots (ss), while the $F_1$ male (Ss) appeared normal even though it was heterozygous for red spots and black ones. The offspring from five pairs are given in Table V, and the same result is evident as enumerated for Table IV. There were likewise two kinds of females, red spotted (Ss) and black spotted (ss) ones, while the males were as usual of the wild type but carried two sets of factors (Ss, ss). These three different phenotypes manifest again a 1:1:2 sex-limited ratio.

The third back cross test consisted in mating an $F_1$ red spotted (Ss) female with a wild-type male homozygous for (SS). The five pairs mated again gave a 1:1 sex-limited ratio for their offspring. Table VI shows that

### TABLE V

### BACK CROSS TEST

*Reciprocal Cross*

$P_1$ 1 Black-spotted Female (ss), × 1 Wild-type Male (Ss)
$F_1$ as follows:

| Pedigree Number of the $P_1$ Pairs | Females | | Males Wild Type (Ss, ss) |
|---|---|---|---|
| | Red Spotted (Ss) | Black Spotted (ss) | |
| 106.2 | 8 | 9 | 19 |
| 106.3 | 9 | 10 | 20 |
| 106.4 | 15 | 14 | 33 |
| 106.5 | 20 | 21 | 40 |
| 106.6 | 29 | 26 | 51 |
| Totals | 81 | 80 | 163 |
| Calculated | *81* | *81* | *162* |

the females were all red spotted (SS, Ss) and every male was of the wild type but carried the same factors (SS, Ss) as the females.

### TABLE VI

### BACK CROSS TEST

$P_1$ 1 Red-spotted Female (Ss), × 1 Wild-type Male (SS)
$F_1$ as follows:

| Pedigree Number of Each $P_1$ Pair | Females Red Spotted (SS, Ss) | Males Wild Type (SS, Ss) |
|---|---|---|
| 106.1 | 18 | 19 |
| 106.10 | 29 | 33 |
| 106.11 | 19 | 16 |
| 118.9 | 43 | 41 |
| 118.8 | 35 | 30 |
| Totals | 134 | 139 |
| Calculated | 136.5 | 136.5 |

The final back cross test was the reciprocal of the one just described, a pure red-spotted (SS) female being mated to a heterozygous (Ss) $F_1$ wild-type male. The total offspring from five such pairs approximate again a 1:1 sex-limited ratio (Table VII) because all the females were red spotted (SS, Ss) and the males were again of the non-spotted wild type, but carried the identical genes (SS, Ss) as their respective females.

TABLE VII

BACK CROSS TEST

*Reciprocal Cross*

$P_1$ 1 Red-spotted Female (SS), × 1 Wild-type Male (Ss)
$F_1$ as follows:

| Pedigree number of each $F_1$ pair | Females Red Spotted (SS, Ss) | Males Wild Type (SS, Ss) |
|---|---|---|
| 100.1 | 23 | 24 |
| 100.2 | 32 | 30 |
| 100.3 | 41 | 45 |
| 100.4 | 39 | 42 |
| 100.5 | 27 | 23 |
| Totals | 162 | 164 |
| Calculated | 163 | 163 |

## CONCLUSIONS

In our cultures of *Bruchus quadrimaculatus,* the so-called "four-spotted cowpea-weevil," the wild insects have a tan body and elytra color for both male and female and, further, every female of such stocks has four black spots, two on each elytrum, but the males are non-spotted.

In a culture pure for red body and elytra was found a female having four red on her elytra instead of the usual four black spots. This unusual type proved to be the result of a mutation from black spots to red spots. Pure cultures of this red-spotted mutation showed the same degree of sex limitation as the black spotted wild type, because its males were likewise non-spotted.

Lastly, the gene for red spots is a complete dominant to the black-spotted factor. Here also is further evidence that dominant mutations are not uncommon in *Bruchus* because the three mutations described previously and the one in this paper are complete Mendelian dominants.

# A SIMPLE FORMULA GIVING THE NUMBER OF INDIVIDUALS REQUIRED FOR OBTAINING ONE OF A GIVEN FREQUENCY

PROFESSOR H. J. MULLER

UNIVERSITY OF TEXAS[1]

It often happens in genetic work that a cross is made for the purpose of producing—or testing the possibility of producing—a particular type of individual, when a given frequency of occurrence of such individuals is expected on the basis of certain *a priori* considerations. Thus, let us say that it is expected theoretically that one among sixty-four of the progeny may be of the desired type. The question then arises, how many individuals should we prepare to raise in order to be sure of securing at least one of the kind sought for—provided our theoretical expectation is correct. An extremely simple calculation gives the answer, after we have defined the word "sure"—which otherwise is inexact, since there is no such thing as perfect certainty. If we define sure as meaning 99 chances of success to one of failure—*i.e.*, a chance of failure ($F$) of only .01—then we must raise 4.6 times 63½ individuals (or 292) to be "sure" of getting the special one sought for. And in case such an individual then fails to appear, it will be "proved" (made highly probable) that the theory that gave the expectation one in 64 is incorrect. If, to take another example, we were looking for a particular crossover combination that we expected just once among each thousand offspring, we must prepare to get 4.6 × 999½, or 4598 offspring, to be similarly sure of securing one of these crossover individuals.

Even where a large proportion of the "desired" individuals are expected, such as one among every two or three of the total number, the question raised above still remains important in those cases in which the individuals cannot be classified by inspection alone but must be tested to determine their composition. For then our formula will tell us the minimum number of individuals which it is necessary to test, in order to be sure to include one of the kind desired. Thus, for instance, suppose we wished to inbreed a homozygous dominant derived from an $F_2$ plant population of the type 1AA : 2Aa : 1aa; how many individuals of the dominant type must we inbreed in order to be sure that we are including one homozygote? Since one among every 3 dominants is of the required homozygous kind, the number that must be bred is, according to our previous method of calculation, $4.6 \times 2\frac{1}{2}$, or 11.5 (12 to be safe). Or if a back cross had been made, giving a ratio of one heterozygous to one homozygous dominant indistinguishable from each other (one heterozygote among every two individuals), we should have to test $4.6 \times 1\frac{1}{2}$, or 7 individuals, to be sure that we were breeding from at least one heterozygote (or homozygote).

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[1] Department of Zoology, Contribution no. 160.

The number 4.6 is the (negative of the) natural logarithm ($\log_e$) of .01, the chance of our failing to get any individuals of the desired kind; it may be found either by looking it up directly in a table of natural logarithms or else by looking up the common logarithm ($\log_{10}$) in an ordinary logarithm table, and multiplying its numerical value (in this case 2.00) by 2.30, the coefficient which converts common to natural logarithms. If, now, our standard of certainty were lower, so that we were satisfied with a chance of success of nine out of ten—or a chance of failure ($F$) of .1 instead of .01—we should have to use the (negative of the) natural logarithm of .1, which is 2.3, instead of 4.6. In that case $n$, the number of offspring to be raised, in the first example above would have been $2.3 \times 63\frac{1}{2}$, or 146; in the second example $n$ would have been $2.3 \times 999\frac{1}{2}$, or 2399; in the third example $n$ would have been 5, and in the fourth between 3 and 4.

We may sum up all of this in the formula:

$$n = -\log_e F(P - \tfrac{1}{2}), \qquad (1)$$

where $P$ is the expected number, such as 64, 1000, 3 and 2, respectively, which on the average will include one individual of the "desired" type. (It will be observed that $P$ is the reciprocal of the chance that any one individual shall be of such type; the latter chance is usually designated as $p$, so that $P = 1/p$.) As any one investigator commonly tries to retain the same standard of certainty (or "chance of failure," $F$) throughout most of his experiments, it will only be necessary for him to remember the one number for $-\log_e F$ (such as 4.6); he may then multiply this same number by whatever $P - \frac{1}{2}$ he is dealing with, and so obtain $n$ directly, without recourse to logarithmic or other tables, or to any calculations.

The above formula is also useful in a somewhat different connection. Sometimes the cross has been already performed, or the number involved can not be exactly controlled, so that $n$ is given. If no individuals of the type in question have appeared among this number, the problem is then raised, has our theoretical $P$ (or $p$) been disproved by the results or not; *i.e.*, what was the chance ($F$) of this failure to obtain any "desired" individuals, on the supposition that our $P$ had been correct? Here, then, $n$ and $P$ are given, and $F$ is to be found. From formula (1) we find that

$$\log_e F = -\frac{n}{P - \frac{1}{2}} \tag{2}$$

Having thus found $\log_e F$, we may look up $F$ itself in a logarithm table. In terms of common logarithms we have:

$$\log_{10} F = -\frac{n}{2.3(P - \frac{1}{2})}.$$

As an example, we may imagine that a group of 60 $F_2$ has been counted, and that all these are of the dominant type. Certain theoretical considerations may have led us to expect that either a ratio of 15 dominants: 1 recessive ($P = 16$) or all dominants would obtain. We may then ask, do the results disprove the 15:1 interpretation, *i.e.*, just what would have been the likelihood of getting this result if $P$ had been 16. This likelihood is what we have called $F$, and by our formula

$$\log_{10} F = -\frac{60}{2.3 \times 15\frac{1}{2}} = -1.683.$$

For use in a logarithm table this number is then changed to the form $-2 + .317$. We now find in a table of common logarithms that $F = .02075$. Hence there was only .02 chance, or one chance in 50, of getting no recessives among the 60 $F_2$ if $P$ had been 16, and, other considerations being equal, we must regard the 1:0 interpretation as being far more probable than that of 15:1.

It may be noted that in cases where $\log_{10} F$ turns out to be less than $-2$, it will usually be unnecessary to look up its value in a logarithm table, for in such cases $F$ must have a value of less than .01, and we can therefore take it for granted without further calculation that the $P$ assumed in the formula was incorrect. Conversely, when $\log_{10} F$ turns out to be greater than $-1$, we know that $F$ must have been greater than .1, and that the assumed $P$ was therefore quite possible. Use of a logarithm table will seldom be required, then, except when $\log_{10} F$ turns out to be between $-1$ and $-2$, and here a small table, containing only 10 values, would ordinarily be quite sufficient to give us the information concerning the probability which is needed.

Blakeslee, Belling, and Harris[2] have recently published tables showing the value of $F$ for all practically possible values of $n$ in the case of seven different values of $P$,—2, 3, 4, 6, 9, 12 and 36, respectively. When $P$ has these values, therefore, these tables may be used in place of formula (2) and logarithm tables, for finding $F$ ($n$ being given). For finding $n$, however ($F$ given), formula (1) will be easier to use than any tables, in the ordinary cases where $F$ has a certain standard value, the log of which may be remembered.

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[2] Blakeslee, A. F., Belling, J., and Harris, J. A., "The Probability Established by a Culture of Given Size that a Mating is Capable of Producing only Dominant Individuals," AMERICAN NATURALIST, Vol. 56, pp. 458–461; Sept.–Oct., 1922.

The formula given is only an approximation; a closer approximation is:

$$n = -\log_e F(P - .51). \qquad (3)$$

As will be shown presently, however, the number of individuals ($n$) as calculated by formula (1) never differs from the true value by as much as half of a single individual, and in all ordinary cases the error is much less even than this; hence, since we cannot deal with fractions of individuals, the number obtained is quite correct for our purpose. In finding $F$, where even less exactness is required, the error is likewise entirely negligible.

We may now give the proof of our formula. Let $1/P = p$, the chance that any one individual shall be of the desired type. Then the chance that any individual shall be of the other (more usual) type is $1 - p$, and $F$, the chance that all $n$ individuals shall be of the usual type, must be $(1 - p)^n$. Taking the log of $F = (1 - p)^n$, we obtain the formula $\log F = n \log (1 - p)$ or

$$n = \frac{\log F}{\log(1 - p)}.$$

This is the strictly accurate formula, which is, of course, well known. It may, however, also be written in the form

$$n = -\log_e F(P - \tfrac{1}{2}) \times \frac{-1}{(P - \frac{1}{2}) \log_e (1 - p)} \qquad (4)$$

(by merely multiplying both numerator and denominator of the expression on the right hand by $-(P - \frac{1}{2})$).

Let us call the true $n$, found by the accurate formula given above, $n_t$, and the approximate $n$ (found by formula 1), $n_a$. Then it is evident from (4) that

$$n_t = n_a \times \frac{-1}{(P - \frac{1}{2}) \log_e (1 - p)}$$

In order to prove, then, that our approximation formula gives nearly correct results, we may prove that, for all values of $P$ which would be used in practice, the factor $-1/(P - \frac{1}{2}) \log_e (1 - p)$ is so nearly equal to 1 that it may be neglected.

Table I shows (in column $A$) the values of this factor,

TABLE I

| Mendelian Ratio | *A* | *B* | *C* | *D* |
|---|---|---|---|---|
| | $\frac{-1}{(P-\frac{1}{2})\log_e(1-p)}$ | Error, in % | Absolute Error of $n_a$ | Absolute Error of $n_a$ when $F = .001$ |
| 1 : 1 | .961 | 3.9 % | $.06 - \times -\log_e F$ | .39 |
| 2 : 1 | .987 | 1.3% | $.03 + \times -\log_e F$ | .23 |
| 3 : 1 | .993 | 0.7 % | $.02 + \times -\log_e F$ | .17 |
| 7 : 1 | .9985 | 0.15% | $.01 + \times -\log_e F$ | .08 |
| 15 : 1 | .9996 | 0.04% | $.01 - \times -\log_e F$ | .04 |
| 31 : 1 | .9998 | 0.02% | $.01 - \times -\log_e F$ | .04 |
| 63 : 1 | .9999 | 0.01% | $.01 - \times -\log_e F$ | .05(±) |

for a number of the commoner Mendelian ratios, together with (column *B*) the percentage[3] deviation of the factor from 1. It will be seen that the percentage difference between the factor $-1/(P - \frac{1}{2}) \log_e (1 - p)$ and 1 is only 3.9 per cent. for the lowest values of *P*, and decreases as *P* increases. Since, in finding $n_t$, this factor is merely multiplied by $n_a$, it is evident that the percentage deviation of the factor from 1 is the same as the percentage deviation of $n_t$ from $n_a$—*i.e.*, the percentage error of $n_a$. The absolute error in the final result would of course be this percentage × $n_a$ itself, and this absolute error has also been listed in the table (column *C*) in terms of multiples of $-\log_e F$, since the latter may be different in different cases. In practice (when *n* is to be found) $-\log_e F$ would hardly ever have a greater numerical value than 6.9, as this corresponds with a chance of success of 999:1. In that case, as will be seen from column *D*, the absolute error for the 1:1 ratio—the greatest error of all—would be only .06 × 6.9, or .4 of one individual, and the absolute error in most of the other cases would be less than .1 of an individual, no matter how big *n* itself became. For more usual values of $\log_e F$ the absolute error would be still smaller.

It can be shown algebraically that as *P* increases (*i.e.*, as *p* approaches 0) the value of the factor $-1/(P - \frac{1}{2}) \log_e (1 - p)$ approaches 1 as a limit (and that therefore the approximation formula gives results having a smaller and smaller percentage error as $P$ increases). The proof is as follows:

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[3] Per cent. taken on the basis of the assumed (approximation) value.

$$\lim_{p\to 0} \frac{-1}{(P-\frac{1}{2})\log_e(1-p)} = \lim_{p\to 0} \frac{-1}{\left(\frac{1}{p}-\frac{1}{2}\right)\log_e(1-p)}$$

$$= \lim_{p\to 0} \frac{-1}{\frac{2-p}{2p}\log_e(1-p)} = \lim_{p\to 0} \frac{-2p}{(2-p)\log_e(1-p)} .$$

To evaluate the limit of the latter expression, we may first take the derivatives of the numerator and denominator (since the limit of a quotient equals the limit of the quotient of the derivative of the numerator divided by the derivative of the denominator). Thus we find:

$$= \lim_{p\to 0} \frac{}{(2-p)\frac{-1}{1-p} - \log_e(1-p)}$$

$$\text{(Substituting 0 for } p) = \frac{-2}{2(-1)-0} = \frac{-2}{-2} = 1.$$

$$\text{Wherefore, } \lim_{p\to 0} \frac{-1}{(P-\frac{1}{2})\log_e(1-p)} = 1.$$

Table II is constructed similarly to Table I, but gives the results for the more accurate approximation formula $n = -\log_e F(P - .51)$. It will be seen that little is gained by using the more accurate formula. The approach of the factor $-1/(P - .51)\log_e(1-p)$ to the

TABLE II

| Mendelian Ratio | A | B | C | D |
|---|---|---|---|---|
| | $\frac{-1}{(P-.51)\log_e(1-p)}$ | Error, in % | Absolute Error of $n_a$ | Absolute Error of $n_a$ when $F=.001$ |
| 1 : 1 | .967 | 3.3% | $.05 - \times -\log_e F$ | .33 |
| 2 : 1 | .991 | 0.9% | $.02 + \times -\log_e F$ | :16 |
| 3 : 1 | .996 | 0.4% | $.01 + \times -\log_e F$ | .10 |
| 7 : 1 | .9999 | 0.01% | $.00 + \times -\log_e F$ | .01 |
| 15 : 1 | 1.0003 | −0.03% | $.00 - \times -\log_e F$ | −.03 |
| 31 : 1 | 1.0001 | −0.01% | $.00 - \times -\log_e F$ | −.03 |
| 63 : 1 | 1.00003 | −0.003% | $.00 - \times -\log_e F$ | −.01 |

limit 1, as $P$ increases, and the consequent greater and greater accuracy of this approximation formula, for higher and higher values of $P$, may be proved by a method similar to that used for the other formula.

In the attempt to find the approximation formulæ, the limiting value of $n/P$, as $P$ grew indefinitely large, was first found,—starting with the equation

$$n = \frac{\log F}{\log\ (1-p)}.$$

The limiting value proved to be $\log_e F$ itself. For this evaluation I am indebted to Dr. J. M. Jacobs, of the Department of Mathematics of the University of Texas.

It was then found that when this limiting value, $\log_e F$, was equated to $n/P$, and the equation (in the form $n = P \log_e F$) used as an approximation for finding $n$ in the case of small values of $P$, the errors varied with a regularity such that they could be largely eliminated by substituting $P - .51$ for $P$ itself in the formula. $\text{Log}_e F$ was then seen to be the limiting value of $n/(P - .51)$ also; in fact, any constant may be substituted for .51 and the expression will still have the limiting value $\log_e F$ as $P$ grows indefinitely large, but it was found that .51 is the constant which gives the most nearly correct results for smaller values of $P$.

## Summary

A short approximation formula (see (2)) has been found for estimating the probability of a given expected ratio having been correct, when no individuals of the minority type have appeared. In using the formula for this purpose, it will in some cases be necessary to look up one logarithm, but no other tables and very little calculation are required. The same formula may also be used (in form (1)) to determine the number of individuals that must be raised and classified (by inspection or testing) in order to be sure of finding one of a theoretically given frequency. The calculation for the latter purpose ordinarily consists of only a simple multiplication, without the use of any tables.

# FAMILY RESEMBLANCES AMONG AMERICAN MEN OF SCIENCE

## II. DEGREE OF RESEMBLANCE IN COMPARISON WITH THE GENERALITY: PROPORTION OF WORKERS IN EACH SCIENCE AND DISTRIBUTION OF REPLIES

DR. DEAN R. BRIMHALL
SECRETARY OF THE PSYCHOLOGICAL CORPORATION

THE methods used in determining the number of workers in the various fields of science resulted in distributing the thousand as recorded in the first column of the table below. The second column shows the number of replies from those in the several divisions, of whom, owing to two selections of the group, there were 1,154.

TABLE I

| Science | 1 | 2 |
|---|---|---|
| Astronomy | 50 | 44 |
| Chemistry | 175 | 167 |
| Geology | 100 | 90 |
| Mathematics | 80 | 76 |
| Physics | 150 | 161 |
| Anatomy | 25 | 23 |
| Anthropology | 20 | 18 |
| Botany | 100 | 97 |
| Pathology | 60 | 56 |
| Physiology | 40 | 37 |
| Psychology | 50 | 43 |
| Zoology | 150 | 144 |
| Total | 1,000 | 956 |

It is obvious without expressing the replies in ratios per one thousand that they are evenly distributed, the only variation in any way unusual being those in the physics group, and the relatively large number makes that difference of little consequence.

### RESEMBLANCE IN DISTINCTION COMPARED WITH THE GENERALITY

Two hundred and fifty-six, or more than one in four of those reporting, are known to have distinguished relatives no more remote in relationship than cousin. Table I has given the facts concerning the distribution of replies, showing the evenness of the selection. Table II gives the facts concerning the distribution of those replying and the numbers with distinguished relatives.

TABLE II

| Science | (1) Number Reporting | (2) Number Known to have Distinguished Relatives | (3) Column (2) Reduced to Number per 1,000 | (4) Number of Distinguished Relatives | (5) Number of Distinguished Relatives per 1,000 |
|---|---|---|---|---|---|
| Astronomy | 44 | 10 | 227 | 17 | 386 |
| Chemistry | 167 | 43 | 257 | 96 | 575 |
| Geology | 90 | 35 | 389 | 65 | 722 |
| Mathematics | 76 | 14 | 184 | 28 | 368 |
| Physics | 161 | 38 | 236 | 82 | 509 |
| Anatomy | 23 | 7 | 304 | 11 | 478 |
| Anthropology | 18 | 3 | 167 | 5 | 278 |
| Botany | 97 | 22 | 227 | 36 | 371 |
| Pathology | 56 | 21 | 375 | 39 | 696 |
| Physiology | 37 | 8 | 216 | 20 | 541 |
| Psychology | 43 | 16 | 372 | 28 | 651 |
| Zoology | 144 | 39 | 271 | 71 | 493 |
| Total | 956 | 256 | 267.8±14 | 498 | 521 |

It will be seen that 44 astronomers replied, and that 10 were found to have one or more distinguished relatives of a degree no more remote than cousin. This means that for 1,000 astronomers there would be 227 with distinguished relatives. Of 1,000 chemists 257 would have distinguished relatives, as defined. The average for the twelve groups is shown to be 267.8 with a p.e. of 14. The number of relatives per thousand men reporting is given in the last column. Forty-four astronomers are represented by 386 persons of distinction; 167 chemists by 575 persons of distinction; geology by 722; mathematics by 368, and so on. The average for this set of values is 521. Two hundred and fifty-six men of science have 498 relatives as defined; this is practically two per man. The exact value per man being 1.95 ± .06, using the following values for the twelve sciences as the distribution for which the p.e. is obtained: The number per man for astronomy is 1.7; for chemistry 2.2; for geology 2.1; mathematics 2.0; physics 2.2; anatomy 1.6; anthropology 1.7; botany 1.6; pathology 1.9; physiology 2.5; psychology 2.5, and zoology 1.8.

TABLE III

DISTRIBUTION OF THE BIOGRAPHIES IN "AMERICAN MEN OF SCIENCE," "WHO'S WHO IN AMERICA" AND "APPLETON'S CYCLOPEDIA OF AMERICAN BIOGRAPHY," AND THE STARRED GROUP OF "AMERICAN MEN OF SCIENCE," ACCORDING TO NUMBER IN EACH DEGREE OF RELATIONSHIP.

| | Total in All Three Books | Distribution in the Three Hand-books and in the Starred Group | | | |
|---|---|---|---|---|---|
| | | A | W | E | X |
| B | 146 | 62 | 121 | 18 | 26 |
| Si | 13 | 2 | 13 | | |
| S | 18 | 15 | 13 | | 5 |
| D | 1 | | 1 | | |
| F | 78 | 17 | 40 | 52 | 5 |
| M | 3 | | 2 | 2 | |
| FB | 33 | 1 | 13 | 26 | |
| FSi | 4 | | 3 | 3 | |
| MB | 31 | 1 | 11 | 25 | 1 |
| MSi | | | | | |
| BS | 6 | 5 | 5 | | |
| BD | 3 | | 3 | | |
| SiS | 3 | 2 | 3 | | 1 |
| SiD | | | | | |
| FF | 17 | | | 17 | |
| FM | 1 | | | 1 | |
| MF | 35 | | 2 | 35 | |
| MM | 1 | | | 1 | |
| FBS | 45 | 15 | 37 | 7 | 9 |
| FBD | | | | | |
| FSiS | 15 | 4 | 13 | 2 | 3 |
| FSiD | 2 | | 2 | | |
| MBS | 20 | 7 | 18 | 6 | 4 |
| MBD | 1 | | 1 | | |
| MSiS | 18 | 7 | 16 | 3 | 4 |
| MSiD | 4 | 1 | 4 | | |
| Total | 498 | 139 | 321 | 198 | 58 |

A denotes "American Men of Science."

W denotes "Who's Who in America."

E denotes "Appleton's Cyclopedia of American Biography."

X denotes members of the 'starred' group in "American Men of Science."

At first sight it might seem that the mathematical sciences had a definitely greater number of relatives per man than the more descriptive and biological sciences.

The exceptions in the case of astronomy, physiology and psychology discount the evidence in the other cases. It is likely that a careful analysis of the relation between the number of men reporting relatives and the number of relatives per man would reveal facts of significance. As the figures stand, it seems best to accept them as chance variations.

The range of selection in time and people covered by three handbooks used to determine distinction of those found makes direct comparisons of the totals in Table II less clear than is desirable.

Table III gives the distribution of the 498 relatives listed in Table II and shows (1) the number in each degree of relationship, (2) the number in each one of the three handbooks and the number in the starred group. Thus, there are 146 brothers found in one or more of the three handbooks. Of these, 62 are in American Men of Science, 121 are in "Who's Who in America" and 18 are in "Appleton's Cyclopedia of American Biography." Of the 62 in "American Men of Science" 26 are in the starred group. The significance of Table III lies mainly in the simple way it expresses some of the complicated results of the study. It is an appropriate introduction to the detailed Table IV which follows the account of the duplications in relationship.

## "DUPLICATED" RELATIVES

It is well to call attention to the fact that the word relationships might better be used than relatives. It is quite correct to say that 956 men are known to have 146 distinguished brothers, although six of these brothers are counted twice as brothers and seven are counted again as cousins of 146 distinguished brothers. It may seem illogical to count such cases twice, yet no better treatment is evident. The fact remains that if we consider each person in our group as an individual, there are 146 brothers of these several individuals. If the six repetitions in the brother relationship are to be eliminated, which brother is to be deprived of a relative? The total known repetitions are 31; less than 6.5 per cent. of the 498 relationships.

TABLE IV

| | Distribution of Those Distinguished in Science | | | | | | | | | | Distribution of Those Not Distinguished in Science | | | | Total for Both Groups |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | A | W(S) | E(S) | AW | WE | XA | XAW | AWE | XAWE | Total in Science | W | E | WE | Total not in Science | |
| B | 18 | 10 | 3 | 15 | | 1 | 21 | 3 | 4 | 75 | 63 | 3 | 5 | 71 | 146 |
| Si | | 2 | | 2 | | | | | | 4 | 9 | | | 9 | 13 |
| S | 5 | 2 | | 5 | | | 5 | | | 17 | 1 | | | 1 | 18 |
| D | | | | | | | | | | | 1 | | | 1 | 1 |
| F | 3 | 1 | 14 | 3 | 1 | | 2 | 6 | 3 | 33 | 17 | 21 | 7 | 45 | 78 |
| M | | | | | | | | | | | 1 | 1 | 1 | 3 | 3 |
| FB | | | 6 | 1 | | | | | | 7 | 6 | 14 | 6 | 26 | 33 |
| FSi | | | | | | | | | | | 1 | 1 | 2 | 4 | 4 |
| MB | | | 7 | | 1 | | | | 1 | 9 | 6 | 13 | 3 | 22 | 31 |
| MSi | | | | | | | | | | | | | | | |
| BS | 1 | | | 4 | | | | | | 5 | 1 | | | 1 | 6 |
| BD | | | | | | | | | | | 3 | | | 3 | 3 |
| SiS | | | | 1 | | | 1 | | | 2 | 1 | | | 1 | 3 |
| SiD | | | | | | | | | | | | | | | |
| FF | | | 3 | | | | | | | 3 | | 14 | | 14 | 17 |
| FM | | | | | | | | | | | | 1 | | 1 | 1 |
| MF | | | 10 | | | | | | | 10 | | 23 | 2 | 25 | 35 |
| MM | | | | | | | | | | | | 1 | | 1 | 1 |
| FBS | 3 | 4 | 2 | 3 | | | 9 | | | 21 | 19 | 3 | 2 | 24 | 45 |
| FBD | | | | | | | | | | | | | | | |
| FSiS | 1 | 1 | | | | | 2 | | 1 | 5 | 9 | 1 | | 10 | 15 |
| FSiD | | | | | | | | | | | 2 | | | 2 | 2 |
| MBS | | 2 | 1 | 3 | | | 2 | | 2 | 10 | 7 | 1 | 2 | 10 | 20 |
| MBD | | 1 | | | | | | | | 1 | | | | | 1 |
| MSiS | 1 | 2 | | 2 | | | 3 | | 1 | 9 | 7 | 1 | 1 | 9 | 18 |
| MSiD | | | | | | | | | | 1 | 3 | | | 3 | 4 |
| Total | 32 | 25 | 46 | 40 | 2 | 1 | 45 | 9 | 12 | 212 | 157 | 98 | 31 | 286 | 498 |

Here is shown the distribution of the relatives (1) according to the number in each degree of kinship, (2) according to the number of handbooks in which the biographies are found, (3) the number in the starred group, (4) the number distinguished in science, (5) the number not distinguished in science, although eminent in some other activity than science. In column two under A, we have the number 18. This means that 18 brothers are listed in "American Men of Science" and in no other handbook. W(S) indicates that 10 brothers who were distinguished in science were listed in "Who's Who in America" but in no other handbook. The E(S) means the same for Appleton's "Cyclopedia of American Biography." The other combinations mean that the individual is in the starred group (marked X) and the books represented by the letters. Thus, in vertical column under X·AWE, we have listed the relatives who belong to the starred group and who are mentioned in all three handbooks. The column of totals beginning with 75 gives the number in each degree of kinship who are distinguished in science. The next section to the right gives the same sort of distribution for the biographies of those shown not to be distinguished in science.

All persons counted as belonging to the "science" group have been indicated in the lists by having their names printed in small capitals. Inclusion in "American Men of Science," membership in scientific societies with "performance" qualifications, teaching position in science, university degrees from departments of science, were the criteria on which most of the persons were counted as belonging to the group distinguished for performance in science. Some few, especially those whose records were found only in Appleton's Cyclopedia, were counted as scientific if the descriptive accounts were judged to warrant such inclusion. Where individuals were distinguished in science and other fields as well, they were counted in the first group. A more detailed analysis of the problem of specialization of resemblance is given in a following chapter.

## COMPARISON OF THE BROTHERS WITH THE BROTHERS OF THE GENERALITY

It has been found desirable in the interest of simplicity and accuracy to compare part of the group of brothers listed in "Who's Who in America" with men of the generality. These brothers are those found listed in Vol. 7

(1912–13). The advantages of such a limitation are (1) that the selection is general, that is, it is not limited to one field of activity but is supposed to cover all fields with a measure which includes people of approximately the same minimum grade, (2) the number of living notables in the book may be compared with the generality, and more particularly the number of the same age limits, (3) this volume covers very nearly the exact period at which requests were being answered by the members of the group studied.

Table V gives the distribution of brothers selected in this manner and arranged according to the scientific activity of the men whose brothers they are, also according to the number who have worked in science and the number who have not.

TABLE V

DISTRIBUTION OF BIOGRAPHIES OF BROTHERS IN VOL. 7, 1912–13, WHO'S WHO IN AMERICA

| Science | Number Reporting | Number of Brothers Found Listed in Vol. 7 of W. W. in A. | Number in Science | Number Not in Science |
|---|---|---|---|---|
| Astronomy | 44 | 5 | 3 | 2 |
| Chemistry | 167 | 16 | 8 | 8 |
| Geology | 90 | 14 | 6 | 8 |
| Mathematics | 76 | 5 | | 5 |
| Physics | 161 | 20 | 13 | 7 |
| Anatomy | 23 | 1 | | 1 |
| Anthropology | 18 | 3 | 1 | 2 |
| Botany | 97 | 8 | 5 | 3 |
| Pathology | 56 | 8 | 4 | 4 |
| Physiology | 37 | 2 | | 2 |
| Psychology | 43 | 9 | 1 | 8 |
| Zoology | 144 | 15 | 6 | 9 |
| Total | 956 | 106 | 47 | 59 |

Table V shows that 956 men of science have 106 brothers listed in the particular volume chosen. This volume has a total of 18,794 sketches of which approximately nine per cent., or 1,700, are women. Thus, there are 17,000 of the generality of 1911 who are comparable with 106 brothers of men of science.

The average age at which men become mentioned for the first time in "Who's Who in America" was determined for volume six, and found to be 49.9 years. It would not be far different for the years covered by the next volume. The average age of men of the starred group at the time of the second selection was 48.12 years. In 1911, the time at which the replies to the requests were being received, the men themselves and their brothers would have almost reached this average age at which men are included. The brothers of the men of the starred group are, thus, rather nicely comparable with those included in volume 7 of "Who's Who in America," so far as age limits are concerned.

The selection of a number of men of the generality comparable with the 956 men of science is not so simple. The most reasonable method seems to be that of determining the number of males of the total population in 1911 above the median age at which they first attain a place in the handbook, then adding a like number from the total of the male population below this point. Use of this method gives a total of approximately 14,000,000 males for the group who are comparable with men in "Who's Who in America" and the men of science.

There are approximately 17,000 men of the "Who's-Who-in-America" grade and 956 men of science who are comparable so far as the age factor is concerned, with 14,000,000 males of the generality. Among the 14,000,000 males of the generality 17,000 are distinguished by having biographical accounts in "Who's Who in America." The average man of the group comparable with the men of science had, therefore, one chance in 823.5 to be included in that book. One thousand men of the generality had a little more than one and one fifth (1.214) of a man included.

How do the brothers of distinguished men of science fare? According to the data presented by the men themselves on number of living brothers and the number found to be distinguished by the writer, 1,000 brothers of distinguished men of science have 87.75 among them who are distinguished as defined. The ratio of these two proportions, 1.214 and 87.75, is as 1 to 72.78. According to these figures, if two men, one a brother of a man of science and one a man of the generality, shake dice for distinction, the brother of the man of science would win nearly 75 times to one winning by the man of the generality.

How were these ratios obtained? Nine hundred and fifty-six men of science were found to have 106 brothers with biographical histories in "Who's Who in America" in Vol. 7, 1912–13 (Table V). This gives a ratio of 110.88 per thousand. Eight hundred and eighty-four men reported having 1,726 brothers, of whom 1,107 were living at the time of the report in 1910–11.

One thousand men of science would, therefore, have 1,263.6 brothers living at the time in question, of whom 110.88 or 87.75 per one thousand would be distinguished. The ratio of 17,000 in "Who's Who" to the comparable group of the generality, 14,000,000, being 1.214 per thousand, the brothers of men of science are, under the given conditions, 72.78 times as likely to become distinguished as the men of the generality.

There are factors tending to make this difference too small. Deaths of some of the brothers may have been omitted. Of this Cattell has said in his discussion on vital statistics:

> It is difficult to see how more valid statistics can be obtained than those supplied by scientific men, the order of birth, the dates of birth and death having been given; yet it is undoubtedly the case that all deaths are not recorded, especially for the brothers and sisters who died in infancy.[1]

A second factor is that of omissions in cases of distinguished brothers. Some few may have escaped notice in the search for those recorded in the particular volume used, but it is thought that there were few so omitted. It is true that the original reports failed to give anything like a complete account of the relatives who were known for their special performance in the various activities of life. A great many were reported who were not found recorded in any handbook and this is a feature that is of considerable importance, but it is a fact that but 84 brothers were given in the original reports who were found to be distinguished, while 146 were later found in one or more of the three handbooks used. Twenty-five of these were found to have become known during the course of the investigation, that is, included in editions of "Who's Who in America" for the first time after 1910–11. But if these factors were at work they tended to make the differences less than the figures indicate. The great difference as it stands, 1 to 72.78, is of sufficient validity to point to a resemblance between men of science and their brothers, and resemblance of the generality.

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[1] *Scientific Monthly*, October, 1917.

If we could know the number of brothers the men of the generality had and the number who became distinguished we could express the difference in resemblance of families of men of science and families of the generality. We do not know these facts, but the reader will see that the figures can not be far different from those given for the generality. The men of the generality would have approximately the same number of brothers per thousand as the men of science, and the 17,000 would be distributed among them in the same proportion as they are among the 14,000,000.

Fourteen millions may be a group unfairly large, that is, unfairly large as a number comparable to the thousand men of science. No better method than that used is known. The reader may make whatever selection of the general population he thinks best; he will find a difference that is highly significant, one that can not be explained as a matter of chance.

If 17,000 distinguished men of the generality came from a group of 14,000,000, the 106 brothers of men of science would, as a matter of chance, have had to come from a group of more than 84,000. What this means is that each man of science would have had to have about 80 brothers if the latter were no more likely than a man of the generality to become distinguished. If by some miracle towns and cities competed for honors determined by production of men of science, a country town of 7,000, peopled by families of the grade of brothers of American men of science, would have to be handicapped by putting it with cities having a population of half a million if that competition were to be interesting.

## RESEMBLANCE IN SCIENCE

What is the resemblance in performance in science? Table V gives the distribution of 106 brothers according to the direction of the work of the men whose brothers they are. It also gives the distribution according to two groupings, those whose work has been in science and those whose work has been in fields other than science. Some of those in the first group, the science group, have shown special performance in fields other than science, but none of those listed in the "non-scientific" group is known to have achieved distinction in science. It must also be noted that 28 brothers who have shown special performance in science are not included in this table. They are not included because they are not found in the particular handbook used in obtaining these ratios. Some of the 28 are in "American Men of Science," some are included in Appleton's Cyclopedia and some are in Who's Who of editions other than that used, namely, Vol. 7. The same holds true for biographies of 13 men whose work was not in science. The details of these facts may be seen at a glance in Table IV.

There were, as Table V shows, 47 distinguished in science and 59 who were not distinguished in science. Since there were approximately 2,500[2] or about one seventh of the 17,000 males in Vol. 7 who were workers in science, the chances of a man of the generality becoming distinguished, as defined, in that field is approximately one in 5,600.

It has been shown that 1,000 men of science would have about 1,300 brothers comparable, in age, with 14,000,000 of the generality. Since 956 men of science with *x* brothers had 47 brothers distinguished in science, 1,000 men of science with 1,263 brothers would have 49.2 so distinguished. If but one man in 5,600 of the generality achieves similar distinction, the brother of the man of science is 217 times as likely to become distinguished in science as a man of the generality.

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[2] The biographies of the first 400 pages in Vol. 6 were gone over carefully and the number, per hundred pages, who had done work in science that would merit inclusion in such a book as "American Men of Science" was determined. The number in the remainder of the book was an estimate.

Much might be said about the relative chances of distinguished financiers or industrial leaders and men of science having their biographies recorded in such a handbook as the one used in this investigation. It may be that men of science, being associated with public institutions such as schools, or large industrial laboratories, become known to the public and hence have their biographies recorded, although their performance no more merits it than, say, the high-priced manager of a department store. If such discrimination in favor of university people, especially men of science, exists, it should be determined. The facts are that so far as distinction goes there is family resemblance in the matter of achieving distinction, and that resemblance is greater in the direction of the specialized activity of science. The next section gives additional evidence of this specialized resemblance.

## THE STARRED GROUP

There were 26 of the brothers who were members of the starred group. That is, 26 of the brothers of the men of science belong to the group itself. Three, however, were in the first edition only, leaving but 23 for comparisons with the groups under consideration. Since 23 of the *x* number of brothers of 956 men of science belonged to the starred group, 24 of the 1,263 brothers of 1,000 men of science would belong to the starred group. About two per hundred, or 20 per one thousand belong to the starred group, whereas 14,000,000 men of the generality have one for about 1,150 of their number. The brothers of men of science, therefore, have according to their numbers about 230 times as many of their group belonging to the starred group as men of the generality.

There are in the starred group of relatives 58 relationships; 26 brothers, five fathers and five sons, one uncle, one nephew and 21 cousins. Only the brothers and cousins are comparable groups and the figures show that four fifths as many male cousins as brothers obtained positions in the starred group. There are, however, four times as many male cousins as brothers who have as a matter of chance the opportunity to obtain such a position. This evidence may be used as the reader sees fit. He may explain the difference in terms of nepotism or as congenital equipment which in turn may be explained by similarity in germ plasm which varies directly as the nearness of blood relationship. The figures show that a brother of a starred man is five times as likely to belong to the starred group as a male first cousin.

## SISTERS

In Table IV will be found the distribution of the biographies of the 13 sisters who are known to be distinguished. All 13 are found in "Who's Who in America," but only 11 are recorded in Volume 7. By the use of the method employed in the selection of the 14,000,000 of the generality for comparison in the case of the brothers, there would be found approximately 13,000,000 females for a similar comparison for the women. Since the number of women in Volume 7 of "Who's Who" is approximately 1,700, the relation between the number of women who achieve distinction and the number who are of the same average age limits is found to be as one is 7,647, or .131 per thousand. Ten thousand adult women of the age limits assumed would, according to these figures, be represented by one and a third of their sex. Ten thousand men of the grade of our group would have, according to the figures above, 115 distinguished sisters. This seems to be a startling difference in spite of the small number of cases of sisters.

There were 884 records of men who reported the facts concerning sisters living in 1910–11. They reported having 1,043 living at that time. If this number is correct, 1,000 men would have had, approximately, 1,180 sisters, of whom 11.5 would be distinguished. Since 11.5 in this number, or 9.28 per thousand were distinguished, in the same sense that .131 of the generality were distinguished, a sister of a starred man of science is 70.8 times as likely to achieve distinction as a woman of the generality.

It would be uncritical to make much of the close resemblance betwen the two values obtained in the matter of resemblance of men of science to their brothers and sisters. The fact that the number turns out to be approximately 70 in both cases is interesting and perhaps significant in spite of the small number of sisters found in the handbook used.

It is not known what per cent. of the women of distinction are workers in science but certainly not ten per cent. About five per cent. of the persons included in "American Men of Science" are women. Four, or over a third of the eleven of the sisters are known for their work in science. Here again, in spite of small numbers, the evidence of family resemblance is in the direction of specialized performance.

## Fathers

There were 944 replies giving the necessary vital statistics of the fathers living in 1910–11. There were 246 reported living. There were 29 of these 246, or, 117.9 per thousand included in Volume 7 of "Who's Who in America." Eleven, or over one third, were distinguished in science. On first thought it might be supposed that this is evidence of a greater resemblance between men of science and their fathers than between themselves and brothers. This, of course, would be a difficult matter to explain in organic terms. The greater the number of years a man lives, the greater his opportunity, other things being equal, of obtaining a place in the ordinary biographical handbook. The chances of a person who dies at 20 are practically nil. Relative length of life may be the explanation.

## MOTHERS

Three mothers of the 956 are known to be distinguished. This number, though small, is significant. The reader may be interested in turning to Table IV and noting the number of distinguished brothers and fathers of the mothers.

Social inheritance, such as family tradition, family wealth and occupation may direct the activities of an individual. It may be that families with university traditions have a very special advantage over the ordinary family in its chances for distinction. If this is so, more people should have the opportunity for university traditions.

## SUMMARY

The investigation has shown: (1) That more than one man in four of the starred group of American Men of Science is related to one or more persons of distinction as defined; (2) that for one particular measure of distinction, the brothers of men of starred group are approximately 70 times as likely to become distinguished as a man of the generality; (3) that the resemblance is in the direction of the performance as well as the quality as shown by the number of brothers distinguished in science, being for the brothers 217 times that of the generality; (4) that the resemblance within the starred group gives additional evidence of specialization in similarity, being for brothers 230 times that of the generality and four times that of cousins; (5) that the data on the sisters closely approximate the figures on the brothers, though the number involved is small—the figures go to show that the sisters were approximately 70 times as likely to become distinguished as women of the generality; (6) that the direction of the performance was again favorable to science, being one third of the total, but that the small number concerned makes significance questionable; (7) that 29 of the 246 fathers or 117.9 per thousand of those living at the time of the investigation were men of distinction; (8) that three mothers were women of distinction.

*(To be continued)*

# SHORTER ARTICLES AND DISCUSSION

## LONGITUDINAL DIVISION OF THE TENTACLES OF HYDRA FUSCA

SINCE about the middle of the eighteenth century there have been frequent references to the occurrence of branched tentacles in Hydra. At least three naturalists of that period (Baker,[1] Rösel von Rosenhoff,[2] Trembley[3]) have left records of the observation of such abnormalities. Wetzel[4] observed branched tentacles on his experimentally treated animals and on at least one not so treated. He found in this last case that the phenomenon was due to the process of fusion of two neighboring tentacles. Rand[5] found several cases of fusion of tentacles during the course of his experiments with this animal. While carrying on similar experiments Parke[6] observed frequent cases of branched tentacles. Here, too, the branched appearance was due to a stage in fusion. Leiber[7] found a Hydra with two "heads." Each "head" bore, among other normal tentacles, one which was branched. Leiber thought, since the body was dividing, the tentacles must also be undergoing division. He could not be certain, however, because he neglected to count the tentacles at the beginning of his observations. Koelitz[8] observed forked tentacles and found the forks fusing into a single structure. Koch[9] found forked tentacles and regarded them as stages in fusion. Several investigators, among whom are Jennings,[10] Parke,[6] Leiber,[7] Korschelt[11] and Koelitz,[8] have reported cases of longitudinal division of the column of Hydra but so far as I have been able to determine, with the possible exception of Leiber, no one had witnessed such a process in the tentacles of this animal prior to the observations I desire to place on record at this time.

On December 2, 1918, while using some Hydras for class work obtained from Powers and Powers, Lincoln, Nebr., some weeks before, I had my attention called to two individuals each of which possessed one bifurcated tentacle among others of normal appearance. One of these animals was lost by the student who discovered it; the other was isolated and set aside for observation. At that time it was possessed of four normal tentacles in addition to the bifurcated one. Unfortunately, this animal was forgotten for four days. When examined it presented a most remarkable appearance. Altogether, there were fourteen tentacles present, but these were varied in position and form. Five were normal in appearance and position, five were normal in position but reduced in size, two were above the tentacle zone upon the hypostome and reduced in size, and the remaining two were below the tentacle zone and somewhat reduced in size. A bud attached to the parent possessed four normal tentacles and a very short one, all in the usual position. Further observations were cut short by the death of the animal before any further significant changes took place. From subsequent observations, however, I think there is little doubt that the increase in the number of tentacles occurred as a result of longitudinal division.

A thorough examination of all my cultures was then made with the hope of discovering more animals in this interesting condition. No more were found until December 30. I then found one animal which possessed two normal tentacles, two attached at the distal ends and one which was bifurcated near the distal end. This Hydra did not long survive and died unchanged.

The following day an individual was found which not only showed the desired characteristics but which was also in a fairly vigorous condition and lived long enough for me to make certain very interesting observations on the course of division of the tentacles. When discovered this animal had eleven tentacles of three sorts. Six of these were normal, two were reduced in size and insecurely attached to the body and three were bifurcated at different distances from the base. Frequent observations were made on the animal during the next few days. During this time three tentacles completely divided and one other partially so, leaving no doubt as to the general method involved. The plane of division was usually parallel to the antero-posterior axis of the body but in one case the plane of division was at right angles to this with the result that at the completion of the process one of the new tentacles was displaced some distance upon the hypostome. This displacement was probably made more pronounced by cell movement and rearrangement in that region. In one other instance before a tentacle had quite completed division one of the new appendages thus produced began another division, but the second branch persisted for only a short time and then was pinched off and disappeared. No cases of fusion of the tentacle were found at any time. In addition, however, to the process of division of the tentacles this animal also showed a remarkably rapid resorption of these appendages. Indeed, at the end of the period of observation, in spite of the rapid division, so much resorption took place that there remained but six tentacles all apparently normal.

On January 10, 1919, another animal was found showing something of the same peculiar division process. This Hydra possessed three normal tentacles and two more joined at the distal ends. These, I should say, must have arisen from the division of one for the process went on until the two were nearly separated when they broke apart, leaving a portion of one attached to the other. Of course in this case the division did not start at the distal end as usual but somewhere below after which it proceeded distally or possibly in both directions.

Although I have repeatedly searched through my cultures during the past three years no animals showing the peculiarities described in this paper have since been found, with one exception only. This one Hydra was found in March of the present year and showed about the same condition as the animal last described above. I was not able to study the animal and so, of course, I am unable to state whether in this case the split tentacles arose as a result of fusion or actual division.

It has been suggested by Koch[9] Frischholtz[12] and others that overfeeding and sudden changes in temperature may cause resorption of tentacles, and longitudinal division of the body of Hydra. My animals were kept in a fairly constant temperature and fed frequently but not richly upon Cyclops and other small crustacea. So far as I know there were no particularly abnormal conditions.

ALBION COLLEGE

A. M. CHICKERING

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## MICROSCOPICAL METHODS USED IN EXAMINING CHROMOSOMES IN IRON-ACETOCARMINE

FOR nearly three years I have been counting and observing the chromosomes in pollen-mother-cells and pollengrains of Datura,[4] Canna,[3] and other flowering plants, after fixing and staining with iron-acetocarmine.[2] During this time it has been found advantageous to adopt those particular microscopical methods which successive experiments showed to be best fitted for the observation of chromosomal structure in a fluid differing little from water in its refractive index.

Miss N. M. Stevens[10] and others who have extensively used the acetocarmine method for the examination of animal chromosomes seem to have employed oil-immersion objectives, with or without an oil-immersed aplanatic condenser. Excellent work has been, and can still be, done in this way. However, if the same microscopical methods are employed for observing chromosomes in diluted acetic acid of refractive index about 1.35, as for objects in xylol-Canada balsam with a refractive index of say 1.52, then it seems that the full possibilities of the iron-acetocarmine method will not be reached. In the first case the contrast between the chromosome and the medium is one both of color and refractive index, in the second case the contrast is almost wholly one of color.

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* These papers were not available for reading. I have quoted from other authors.

The usual theoretical view is that the resolution, and hence the useful magnification, depends, other circumstances being similar, on the working aperture; that is, half the sum of the utilized aperture of the condenser and the whole aperture of the objective. This seems to have stood the test of experiment.[6] Hence to increase useful magnification, with chromosomes in 45 per cent. acetic acid, and with an oil-immersion objective and condenser, the condenser would naturally be connected with the slide by immersion oil or by water. The former method has only a slight advantage here, and experience shows it cannot conveniently be used where large numbers of slides are daily examined, because of the time spent in cleaning slides, stage, and condenser from immersion oil. With either an oil-immersion or a water-immersion objective, used on objects in water or fluid of similar refractive index, water can, without any marked loss, be used instead of oil to connect the condenser with the slide, and the drying of the condenser and slide with blotting-paper requires but little time. If the slide is too thin, a blank slide of the right thickness is put under it, and connected with it by distilled water.

When an aplanatic condenser of high aperture is focussed, an image of the source of light (flame, white cloud, doubly ground glass, etc.) is, of course, formed in the exact plane of the object. So much of this image as fills the field of view of the eyepiece is utilized, but the outlying unutilized parts often cause a slight fog over the image of the object. If all or most of these outlying parts are cut off by a diaphragm (close to the ground glass or flame) I find, as others have found, that the image of the object is usually sharpened,[1] the utilized aperture of the condenser being unchanged.

With the ordinary plane mirror of the microscope, with an angle of incidence of about 45 degrees, there are usually two fairly bright images of the source of light besides the one primarily reflected from the silver. These two extra images partly neutralize the advantages of the employment of an achromatic or aplanatic condenser. They can be removed, with marked gain, by using a right-angled reflecting prism,[8] which I find about as easy to manipulate as the ordinary plane mirror. If it is fixed on the blackened surface of the plane mirror one hardly notices the change, except by the increased light in the single image. This prism need be no wider than the lowest lens of the condenser.

A yellow-green light filter, used between the ground glass of the lamp and the mirror or reflecting prism, has the following well-known advantages.[9] (*a*) Transmitting mainly the color for which ordinary achromatic objectives are corrected, its use makes them nearly equal to apochromatics. (*b*) Those with experience of it will I believe mostly agree that the yellow green is more grateful to the eyes, especially if microscopical work occupies several hours daily all the year. (*c*) The yellow-green screens being partly or wholly opaque to red light, the carmine-stained chromosomes will be dark or black, and markedly sharper in outline, even with apochromatic objectives. (*d*) If the yellow green has a higher average wave frequency than the artificial light used, then resolution is increased. (*e*) The use of several grades of green screen of different depths of color will serve to increase or decrease the intensity of the transmitted light, while the most suitable aperture in the condenser is retained unaltered. I find the following series of the Wratten gelatine films[7] a useful one (and it includes the three which Spitta[9] found best); namely numbers, 66, 56, 57A, 58, and 61. These transmit respectively, 58, 48, 34, 23, and 18 per cent. of the incident light.[11] (Number 66 is usually somewhat too light for the Mazda C lamp, and number 61 may require the arc.) These films are mounted with balsam between two pieces of parallel-plane glass.

After using the monocular microscope nearly every working day for two years, and the binocular eyepiece for nearly a year, I consider that the gain in easy visibility resulting from the employment of both eyes more than counterbalances any slight defects of the binocular. The binocular image is more vivid, as Jentzsch[5] stated, despite the double reflections and the thickness of glass traversed by the light, than the one-eye image of the old pattern. The tube-length of the binocular may be increased, when necessary, by fitting detachable collars of appropriate depth to the eyepieces.

The oil-immersion objective, achromatic or apochromatic, has been calculated and constructed by the makers primarily for the observation of objects in Canada balsam, or in media of similar refractive index. Therefore if a stratum, one or more hundredths of a millimeter thick, of water, or of a fluid approximating water in refractive index, such as 45 per cent. acetic acid, lies between the coverglass and the object of an oil-immersion objective, the definition is more or less impaired by spherical and chromatic aberrations. As is well known, the spherical aberration can be partially compensated by sufficiently increasing the tube-length of the microscope. It is also a familiar fact that good definition can be obtained under these circumstances if the object is in close contact with the coverglass. But a water-immersion objective, with an aperture of 1.20 or 1.25, only requires correcting by setting the graduated collar to the thickness of the particular coverglass in use, and may then, of course, be focussed down for several hundredths of a millimeter through a liquid of refractive index approximating 1.33, without a perceptible loss of definition. The measurement of coverglass thickness takes only a few seconds, and consists in screwing down the graduated fine adjustment from the upper to the lower surface of the coverglass, and taking the required thickness from a previously prepared table. In checking such a table the Abbe test plate is useful. I find it quicker and more accurate to measure the coverglasses than to set the collar by trial of the best definition. If water-immersion objectives without correction collars are used, of course coverglasses of approximately 0.17 mm. must be selected, and the slight final adjustments are made by increasing or decreasing the tube-length.

In the daily routine of searching over many preparations of chromosomes under large coverglasses, two objectives at least are necessary; a finder, and an immersion lens of the highest attainable aperture. If an oil immersion is used, everyone has had the experience that the definition of the finder is annoyingly marred by the traces of oil on the coverglass; whereas with a water immersion an occasional application of blotting-paper keeps the cover dry and clean. Thus the high-apertured oil-immersion objective is used mainly for the close study of specially selected chromosome groups, which are in contact, or nearly in contact, with the coverglass.

*Summary.*—In the microscopical examination of chromosomes in 45 per cent. acetic acid, it was found more convenient to connect the condenser with the slide by water than by oil; it was usually of advantage to use a diaphragm on the source of light, and when this was done the employment of a reflecting prism was naturally indicated; the green light screens advocated by Spitta were found of quite considerable benefit; the binocular eyepiece was found to add greatly to the vividness and clearness of the image; while the contingent advantages of using a water-immersion objective were considered to repay the trouble of measuring all coverglasses.

JOHN BELLING

CARNEGIE INSTITUTION OF WASHINGTON

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GLOVER M. ALLEN

BOSTON SOCIETY OF NATURAL HISTORY

THE earlier students of geographic distribution, on account of their more limited knowledge of the vertebrate population of the world, were concerned largely with dividing the land masses into realms and provinces which were characterized more or less by the general facies of their faunas. They endeavored to limit these areas by sharply defined boundaries or lines, each to stand, as it were, a sort of zoological Verdun, against which should be written in large letters: "They shall not pass." In later days, with improved methods for intensive collecting, our knowledge particularly of the small mammals has increased a thousandfold, so that the data now at hand are vastly more ample than they were even fifty years ago. We have learned that many of the cherished "lines" and "provinces" are not as clearly marked off as was at first supposed.

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[1] Cambridge meeting, December 29, 1922. The remaining papers will be printed in the issue of THE AMERICAN NATURALIST for May–June.

Two of the pioneers in the modern study of smaller mammals in North America, Dr. C. Hart Merriam and the late Dr. J. A. Allen, have both made extensive contributions to the more exact knowledge of the general distribution of the species on this continent, and have endeavored to define certain climatic zones and their subdivisions, and to refer to each a number of species of birds and mammals that seemed characteristic. Their work is well known and need not be further reviewed beyond saying that Merriam's divisions of North America are tacitly adopted by a certain present-day school of field naturalists as fitting the facts in a general way. These so-called life-zones are really transcontinental and altitudinal temperature belts and are subdivided according to their aridity or humidity. But although temperature is an important element in geographic distribution, it is after all but one of many determining factors. In a country of high mountains, the altitudinal zones, corresponding to the latitudinal belts of the continent, are often sharply defined, and have been ably studied in California by Dr. Joseph Grinnell and his associates. In the eastern United States, however, and more particularly in the New England area, where the greatest altitude is but little over six thousand feet, the transition from warm southern climate to cooler temperatures of the north is very gradual, so that the contrasts in faunas are nowhere very sharp.

In any thorough study of the distribution of the mammals of a given area, each species should be considered as being a component part of the fauna. It is customary, however, to pass lightly over many of those whose distribution is general and to lay stress on those whose associational value is more obvious. This I think leads to an exaggerated view of the importance of particular species of more limited range. Of New England mammals the black bear is a species ranging over nearly the entire continent of North America from the highlands of northern Mexico to the Fur Countries, yet the amount of variation it shows is relatively slight. It is an animal of high intelligence, adaptable and versatile, able to live on a varied diet of vegetable as well as animal food, factors all of which are important in permitting it to cover a wide area. The puma is an even wider-ranging mammal, extending as a species from Patagonia to southern Maine, with numerous geographic variants. In a general way its range in New England was more or less coincident with that of the white-tailed deer, on which it largely preyed. It is interesting that it closely resembles the deer in the general hue of its coat, a matter that results perhaps from similar slinking habits in a similar silvan environment.

I wish to speak especially of a certain number of New England mammals that may be ranged in pairs of more or less closely related species whose ranges in each case are practically complementary. That is, one species of each pair is in its general distribution boreal, while the other is equally austral. Two of our common squirrels illustrate this. The red squirrel (*Sciurus hudsonicus* and subspecies) is abundant and characteristic of the transcontinental spruce and pine belt from Alaska to the Atlantic; it is typically a lover of coniferous forests, and depends for a large part of its food on the seeds of various cones. In central and southern New England where hardwood forests in part replace the conifers, it depends partly on the fruits and seeds of other species, but even here is partial to clumps of pines be they ever so scattered. In contrast to this species is the gray squirrel (*Sciurus carolinensis* and races) which is typically a nut-eater, resorting to cones only in times of scarcity. Its range is chiefly southern, from Florida to central New England on the coast, though extending farther north in the interior. The two species meet within our limits, but the northward extent of the gray squirrel coincides rather closely with that of the beechwoods, the red oak and the sugar maple, all of which furnish it with staple food.

A similar complementary distribution is shown by our two flying squirrels. One is a larger, darker animal of essentially northern distribution, found, as a species, from the forested parts of Labrador, westward to Alaska, with a number of local subspecific forms. In northern New England it is the only flying squirrel, and extends as far south as the higher country north and west of Boston, and upon the higher Alleghenies. The other is a much smaller and less darkly colored species whose range is southeastern, from Florida and eastern Texas to central New Hampshire and central Vermont. Its range is thus essentially austral, though in parts of New Hampshire, Vermont and Massachusetts the ranges of both overlap. I know of one locality in the first-named state where individuals of both species came nightly one winter to feed at the same window-shelf on nuts put out for them. We do not know, however, what actual differences in food preference each may have.

Two species of white-footed mice (*Peromyscus*) have a like relation. The northern fir and spruce forest is inhabited by a gray-furred species with a long tail and a skull differing in its proportions from that of the more southern animal. With many slightly different forms, according to local environmental conditions, the first species (*maniculatus*) is found from Labrador to central Maine on this coast, and south along the tops of the higher mountains, westward to the Pacific, from Alaska to southern California. In New England it is not found in southeastern Maine or New Hampshire, nor in Massachusetts except in the higher parts of Berkshire County. The more southern complementary species (*Peromyscus leucopus* and races) extends from Texas and Georgia to central New England and Minnesota with a few poorly marked subspecies. Where the two species meet, the more northern inhabits the cool damp spots along forest brooks, while the more southern is common in drier places, although it has invaded more or less the edge of the other species' range. The two, although superficially much alike, are everywhere perfectly distinct.

Two species of field-mice or meadow-mice (*Microtus*) may be contrasted, though their cases are not exactly similar. One is in general more northern (*M. pennsylvanicus*), ranging as a species from Labrador to the Carolinas and westward across the northern United States to the Rocky Mountains. It inhabits grassy country and swamps, making burrows and runways. The other species is the so-called mole-mouse or pine-mouse (*Microtus* or *Pitymys pinetorum*) of the southeastern United States from Georgia and southern New England westward in bottomlands to the edge of the plains, and even into eastern Mexico. Its more subterranean habits leading to adaptive mole-like modification of the pelage together with slight but essential differences in the enamel pattern of its cheek-teeth are currently regarded as of sufficient importance to warrant its inclusion in a separate genus. The same two groups occur in the Old World, the first, as here, the more northern in its distribution.

Another genus of meadow-mice is *Synaptomys*, the lemming-mouse, which externally looks like a very short-tailed *Microtus*, but it differs widely in the minute structure of the teeth. Two groups are known, both confined apparently to North America, and now considered subgenera. The first (subgenus *Mictomys*) differs from the more typical *Synaptomys* in details of the enamel foldings, and is high northern in distribution. Various more or less nominal species are now known which, in a final estimate, will probably be referred to a single or perhaps two species with various slightly differentiated local races, extending from northern Labrador and the White Mountains of New Hampshire west to Alaska and Washington. The complementary species, *Synaptomys cooperi*, with a few slightly characterized local races, extends from Kansas to North Carolina and northward to Nova Scotia and southern Quebec, where the ranges of the two overlap, that of the more austral species passing well into the cool northern forested country.

The case of our two lagomorphs is again in point. The varying hare (*Lepus americanus* and races) is an animal of the cool evergreen forests from Labrador to Alaska. In New England it follows south along the western highlands and in eastern Massachusetts, Rhode Island and Connecticut is very local, in our extensive white-cedar swamps. Of more southern distribution is the cotton-tail rabbit (*Sylvilagus transitionalis*), an allied but more primitive genus, an animal of more open bushy country, whose range now includes southern Maine, south-central New Hampshire and parts of Vermont. It has probably extended northward slightly in recent decades.

Two species of lynx are found in New England: the larger, more northern is the Canada lynx of the Fur Countries, formerly common in the Maine woods, probably also northern New Hampshire and Vermont. It has been much depleted in numbers with us through persistent trapping and there is much reason to suppose that its place has been largely occupied by the more southern bay lynx, whose range as a species is from Florida and northern Mexico to Nova Scotia on the Atlantic coast, and to parts of California on the western coast. The chief food of the Canada lynx is the varying hare, while that of the bay lynx includes the cotton-tail rabbit. Both form an interesting parallel, that may be further accentuated by the fact that both species of lynx are bob-tailed with long hind limbs, like the rabbits, an adaptation no doubt for quick progress in thick cover.

Our two genera of foxes may be considered here. The common red fox (*Vulpes fulva*) of the north in its various subspecies is abundant from southern Labrador to Alaska, and southward to Virginia. An allied genus, the gray fox (*Urocyon*) is typically southern, but is now found in Connecticut, parts of western Massachusetts, southern Vermont and southern New Hampshire. It has possibly pushed northward slightly in the last century. The largest races are found in the north, with dwarfed forms extending into Central America and even to the coast of southern California.

Another couple is found in our two species of stoats or weasels. The smaller, shorter-tailed species (*Mustela cicognanii*) is abundant in the northern evergreen forests from Alaska to Labrador, southward in the east to southern Connecticut and to some of the higher Alleghenies. It becomes rare south of Massachusetts. In the north it is essentially a mouser, but is also an enemy of the chipmunk and red squirrel. Meeting the range of this species is the larger, longer-tailed New York weasel (*Mustela noveboracensis*), commoner to the south, and ranging eastward to New Brunswick and into central Maine. It is a relentless foe of the cottontail rabbit, and has perhaps extended its range slightly to the northward in the late centuries. In central and southern New England both species occur together. As if in proof of their respective origins, the more northern species invariably turns white in winter like the ermine, even in winters that, in southern New England, may be nearly snowless. The more southern species, on the other hand, although usually turning white in the northern part of its range, does not always do so, and in the south is usually brown in winter.

What then is the significance of the distribution of those species here selected for discussion? In most of the cases, the more northern of each pair has a transcontinental range, within the spruce and fir forest, whereas the more southern counterpart has a more restricted distribution, *east* of the plains, in general corresponding to the hardwood forest area. Several of the more northern species have close relatives in the northern parts of the Old World, whence they may have arrived in late Tertiary times. May it not be that the more southern complementary species, as well as others now of a more or less restricted distribution in the east, are the survivors of a still earlier invasion from Asia and had once a more extended transcontinental distribution, but have since been driven out in the west through progressive desiccation, perhaps since Miocene times, due to the rise of the Rocky Mountain system and the consequent withdrawal of moisture from the prevailing westerly winds? Paleobotanists, reasoning from the known flora of Tertiary times, conclude that in the early Tertiary the hardwood forests, mostly of familiar genera, extended very much farther west, and that even by the Miocene, the northern hemisphere had still a largely cosmopolitan flora. Presumably the characteristic species of mammals accompanied this hardwood forest in its westward extension, but with its retreat eastward, these have been forced to give place to a different set of species, some of which, as the western chipmunks (*Eutamias*) and ground squirrels (*Citellus* and allied genera), are no doubt invaders from Asia in relatively late Tertiary times.

Another interesting point is that the exact southern limit of no two of these northern species is quite the same; nor do the northward boundaries of any two southern species exactly coincide. The explanation is, obviously, that each species has its special requirements and is limited by them. The case of our three New England moles illustrates this fact. All are distinctively of *eastern* North American distribution at the present time. The common mole (*Scalopus aquaticus*) of the south is abundant from eastern Texas and Florida northward to southern Michigan and the southern edge of Massachusetts. It is met by a northern species of a different genus, Brewer's mole (*Parascalops breweri*), which it resembles in a general way, though the two are very distinct structurally. The latter species ranges from southern Canada, south in the east to east-central Massachusetts, apparently not reaching the coast in this state. Southward it follows the Alleghenies to Georgia, at some altitude, however. The ranges do not actually overlap in New England, but there seems to be a slight hiatus between them. This brings us to a consideration of another factor that has a bearing on the distribution, namely, the soil preference of each species, which in turn is perhaps conditioned in part by food. Thus the southern mole tunnels near the surface in light sandy soil, following this in southern New England to the base of Cape Cod and up the Connecticut Valley as far as Springfield and vicinity. Additional data are much desired as to localities in this state. In eastern Massachusetts, the gravelly range of hills stretching southwest from Manomet, near Plymouth, seems to form an effective barrier to its extent northward. The Brewer's mole, on the other hand, is a deeper burrower at times, and seems to affect much more compacted soil, sandy or even gravelly. Our third species, the star-nosed mole, is primarily a species of swamps, with partly aquatic habits. It occurs from Labrador to the Carolinas, but not very far westward.

Our two species of jumping mice—now considered generically distinct—well illustrate the difference in requirements just alluded to. The widely ranging jumping mouse (*Zapus hudsonius*) of our meadows and hay fields is almost wholly confined to grassy lowlands and open sedgy swamps. The woodland jumping mouse (*Napæozapus insignis*), on the other hand, is, as its name implies, a lover of the northern forests, seldom found more than a few yards from the banks of some little woodland stream. What the precise factors are that limit the ranges so closely are still almost unknown to us. A closely allied jumping mouse is found in the mountains of southwestern China, and indicates a general range for the group that must once have been much wider.

Of particular interest is the case of our common white-tailed deer (*Odocoileus virginianus*). In slightly differentiated races it occurs from Panama to New Brunswick, and seems to find its optimum living conditions in the north, where it grows to a large size. Less than a hundred years ago, it was practically absent from much of central and northern Maine and New Brunswick, where now it is abundant, though remains from shell heaps indicate that it ranged normally along the sea coast to Nova Scotia, even in prehistoric times. The chief factor in permitting this extension of range is probably the extermination of its arch enemy the wolf. In deep snow with a light crust, the deer were practically at the mercy of the wolves, and in an unfavorable winter very few could have escaped at the northern edge of the species' range, for the wolves would get every one. Now, however, with the wolf quite gone, the deer easily overruns all northern New England.

Many other cases might be cited of the close dependence of species on particular combinations of factors. It is clear, however, that in any study of distribution, two main considerations stand out, namely, the past history of the species and its particular biologic requirements. These two factors are likely to be different for each species, so that it should be no source of wonder that common boundary lines can seldom be laid down as delimiting the distribution of a given number of species.

# ECOLOGICAL ASPECTS OF BIRD DISTRIBUTION IN TROPICAL AFRICA

JAMES P. CHAPIN

AMERICAN MUSEUM OF NATURAL HISTORY

FOR some years past I have been investigating the avifauna of the Belgian Congo, and the remarks I shall make are prompted by my attempt to divide that broad area into faunal districts, and then to correlate such subdivisions with others extending beyond the Congo borders to the remainder of the continent. I have had to reconsider the faunal areas already proposed by Wallace, Reichenow, Sharpe,[1] and several other authorities. Fortunately, their conclusions need modification only in detail. I shall concern myself rather with the causes responsible for faunal diversity, but in so short a paper it will not be feasible to offer lists of species of birds in justification of my course, or to sketch it in more than its rough outline. My more thorough discussion, dealing particularly with the birds of the Belgian Congo, is shortly to be published in the *Bulletin of the American Museum of Natural History.*

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[1] *Natural Science*, Vol. III, 1893, pp. 105–107, with chart opp. p. 108.

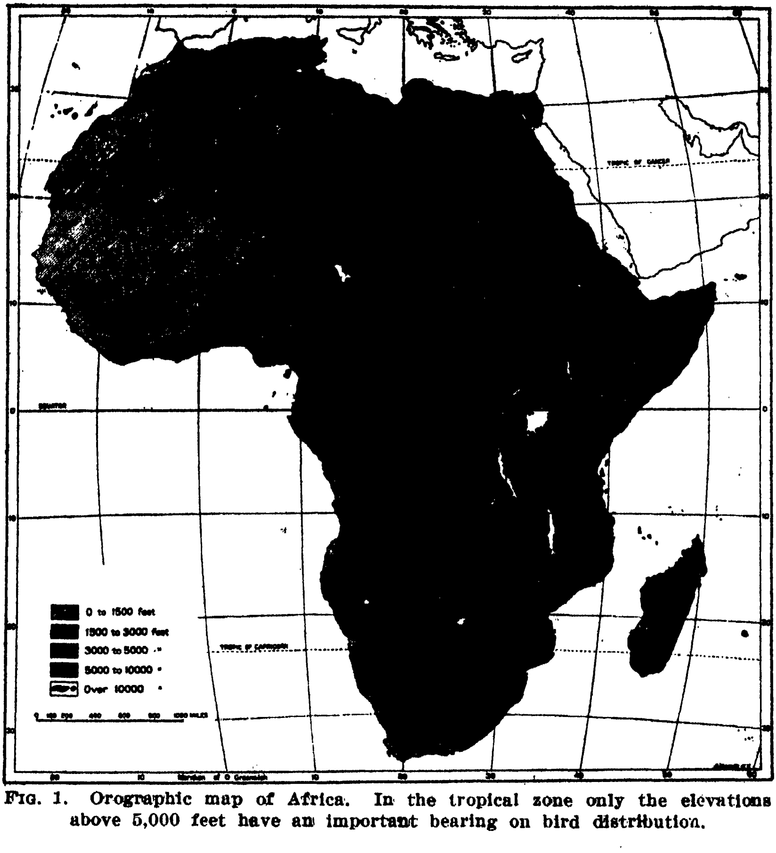

FIG. 1. Orographic map of Africa. In the tropical zone only the elevations above 5,000 feet have an important bearing on bird distribution.

The differences between the avifauna of tropical and southern Africa and that of the adjoining continents and islands are in a great measure the result of isolation by arms of the sea. But when we come to inquire into the reasons for lesser faunal areas upon the African continent, or the contrast, for example, between the faunas of the western and eastern sides of equatorial Africa, we find that the physical barriers alone are scarcely sufficient to obviate extensive mingling of the animals. The key to an understanding of present-day bird distribution in Africa will be found in ecological conditions, especially the nature of the vegetation, which is an index of the climate.

Instead of a lofty mountain chain, like the Andes, Africa has only a broad highland extending from Abyssinia to Nyasaland, through the eastern half of the equatorial belt, and then sending a branch westward to southern Angola, while several disconnected highlands are scattered south of the Zambesi. Africa's high mountain peaks, often of volcanic origin, are isolated, and rise mostly from the eastern part of the continent, though Mt. Cameron and Clarence Peak are to be noted as exceptions.

Where the African highlands rise above 5,000 feet, and receive at the same time sufficient rainfall to support a mountain forest, they exhibit faunal peculiarities; but the number of species of birds whose distribution is thus limited is relatively small. We now know of approximately 1,050 species of birds which occur within the limits of the Belgian Congo. Out of this total, those restricted to the mountains above 5,000 feet, the Kivu volcanoes, the Ruwenzori range, and neighboring elevations, amount to only 92 species. The avifauna of the grassy highlands between 5,000 and 6,000 feet is not unlike that of steppe regions at a much lower level; it is in the mountain forests and the still higher alpine zone that the more typical mountain birds are found.

## LOWLAND DISTRIBUTION

The lowlands of Africa show greater diversity in their birds than do isolated montane areas; and this lowland distribution is much less affected by variation in temperature than by that in humidity. The only barriers discernible are those of vegetation—or the lack of it—resulting from the differences in rainfall.

The life zones which may readily be distinguished at successive levels on many of the African mountains, being largely attributable to changes in temperature, have no near counterpart in the Ethiopian lowlands. Nearly the whole continent lies between the yearly isotherms of 20° Centigrade, which are often taken as the limits of the tropical zone. The northern edge of Africa is excluded from the Ethiopian Region of zoogeographers, but its faunal differences are due to isolation by the arid Sahara and past connections with Europe rather than to lowering of temperature. The southern extremity of the continent is less distinct, speaking ornithologically, because it is not so completely cut off by desert.

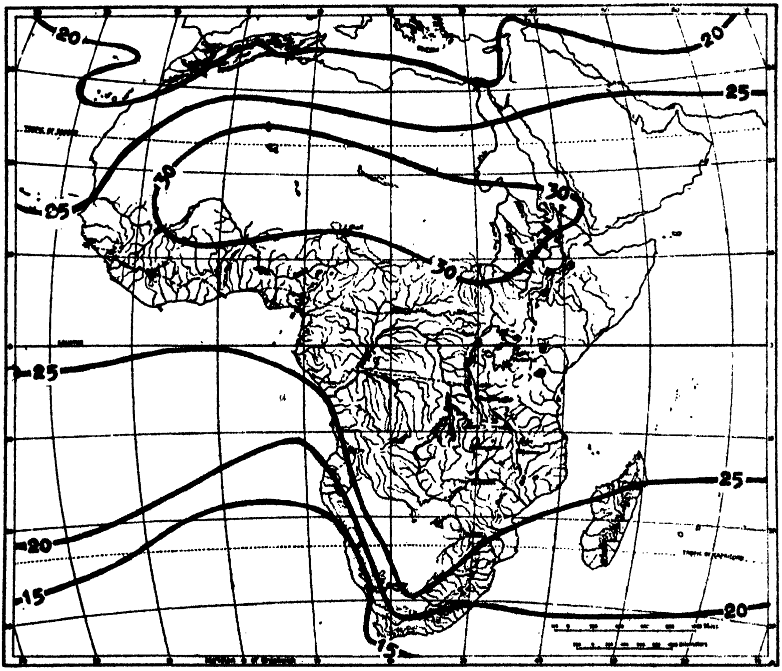

FIG. 2. Yearly isotherms in Africa (from Andree's Hand Atlas).

In my work upon the distribution of birds in the Congo, I was early impressed by the general agreement in dispersal of the bird communities with corresponding plant associations. Fortunately I made the acquaintance in Africa of Dr. Joseph Bequaert, then on a botanical mission for the Congo Museum; and for some years I have been able to compare notes with him, and secure information as to plant distribution.

The whole question of plant and bird distribution in Africa, particularly in the lowlands, goes back to the distribution and abundance of rains. If we examine Knox's rainfall map[2] we find the annual rainfall varying from next to nothing in some of the desert regions (both north and south of the equator) to over 160 inches along considerable stretches of the West African coast. On the slopes of Mt. Cameroon it attains 412 inches. Wherever the rains exceed 60 inches annually, the country is apt to be covered with dense tropical forest, although the seasonal distribution of the rains often holds the balance of power.

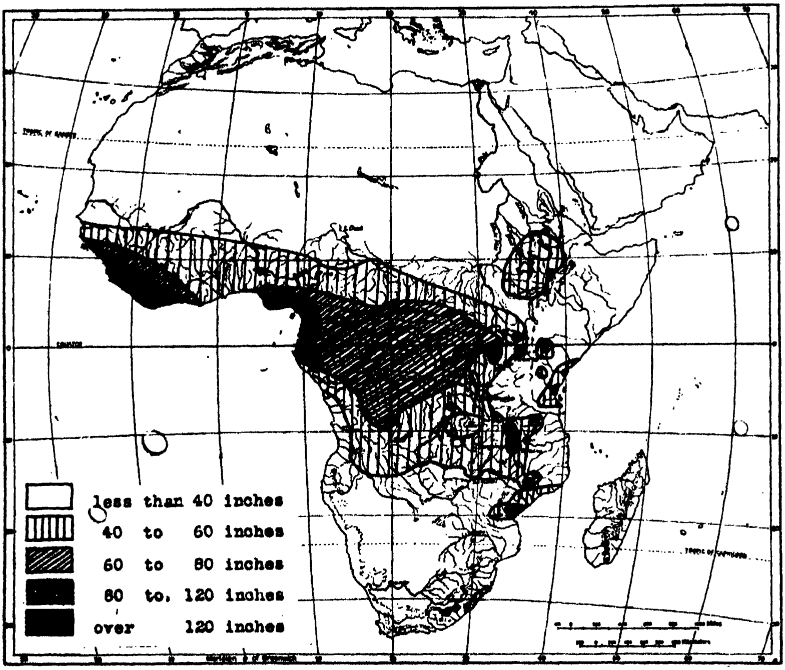

FIG. 3. Total annual rainfall in Continental Africa (after Knox). Note how many points of similarity exist between this map and the avifaunal map in Fig. 11. The seasonal distribution of the rains is next in importance to their total amount.

In Sierra Leone, where there is a dry season of four months, a total annual rainfall of 170 inches does not suffice for a continuous forest growth. Wooded patches are intercepted by grasslands. In parts of the Upper Congo, on the other hand, where the rains scarcely reach 65 inches, a superb, unbroken forest persists because there is seldom a month without rains. Despite the drier nature of eastern equatorial Africa, there are spots with heavy rainfall, due to local topography. They likewise support heavy forest, but more often it is of montane type.

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[2] "The Climate of the Continent of Africa," 1911, Pl. I.

Going from the barren rainless areas of Africa toward the equatorial forests, one finds first grassy steppes, with few trees, widely scattered, and at length a savanna country often bountifully studded with trees, or even wooded. But everywhere there is withal a luxuriant growth of grass beneath the trees, save in

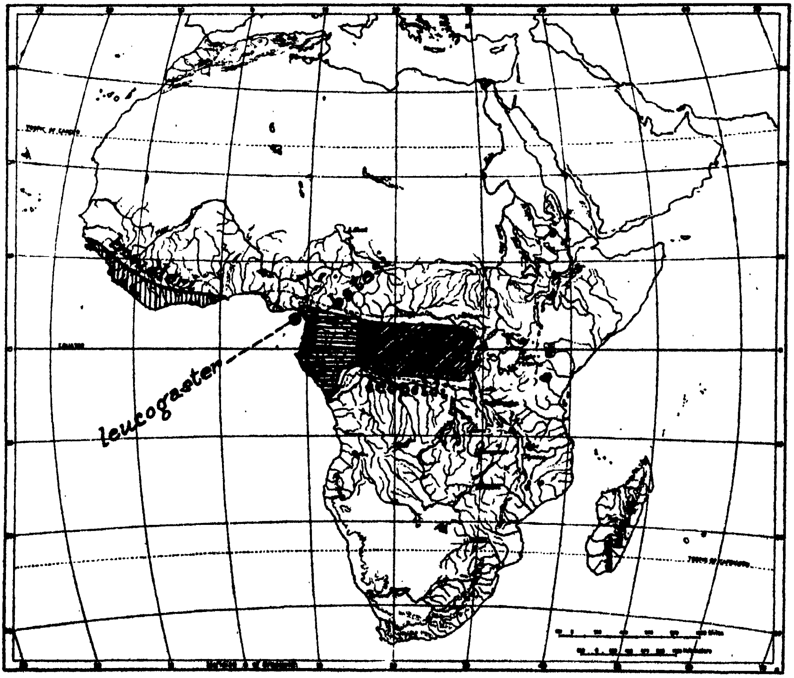

FIG. 4. Distribution of *Corythornis leucogaster*, a small African kingfisher living along brooks only in the dense forest. Four geographic races are recognizable, resulting from partial isolation. They differ from each other in details of color pattern and in size of bill.

especially moist spots like ravines and river-bottoms, which have gallery-forests resembling strips of the equatorial rain-forest. Here the trees owe their luxuriance to ground water. The entire equatorial forest belt is characterized by the extreme scarcity of grasses.

It is through these different types of vegetation that the rainfall determines the distribution of birds. For instance, the forests in many parts of Africa are so extensive that they exclude wholly, from wide areas of the continent, many typical Ethiopian birds, not only such as rely upon grasses for their food, but even fruit-eaters like the colies. The contrasts in preferences as to vegetation are of such weight that we may speak of the African avifauna, with the exception of littoral species, as divisible into forest, savanna, montane, and desert associations. Even the waterfowl show distinct preferences for forest or open country. Hartlaub's duck (*Pteronetta hartlaubi*) is confined to the wooded streams of the West African subregion; whereas the Egyptian goose, like the spur-winged, shuns all but the very broadest rivers of the forest country, for they prefer those of savannas and steppes.

Certain species of birds, nevertheless, are often stated to occupy practically the whole Ethiopian region. In many instances this is erroneous; in the few where it is approximately true, there is a good ecological reason. The hawk, *Kaupifalco monogrammica,* for instance, is able to find subsistence in the clearings of the equatorial forest, whereas in the savannas it will generally be found only where the trees grow thickest, as along the borders of gallery-forests.

To one who studies the birds of the forest at first hand it will be further evident that there is a second-growth association of birds, distinct from those of the virgin forest. Mr. William Beebe[3] has already called attention to this in British Guiana and Mr. G. L. Bates[4] in the Cameroon. Its importance is enhanced by the wasteful manner in which the African native is continually cutting down the virgin forest to establish farms for his plantains, which so soon impoverish the soil that the villages are ever being displaced. The rapid-growing woods, famed in stories of travel, are second-growth, the trees of which have soft, light wood, and never attain the majestic size of the slow-growing virgin forest.

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[3] "Tropical Wild Life in British Guiana," 1917, pp. 60–61.

[4] *Ibis,* 1904, pp. 593–4; 1909, p. 5.

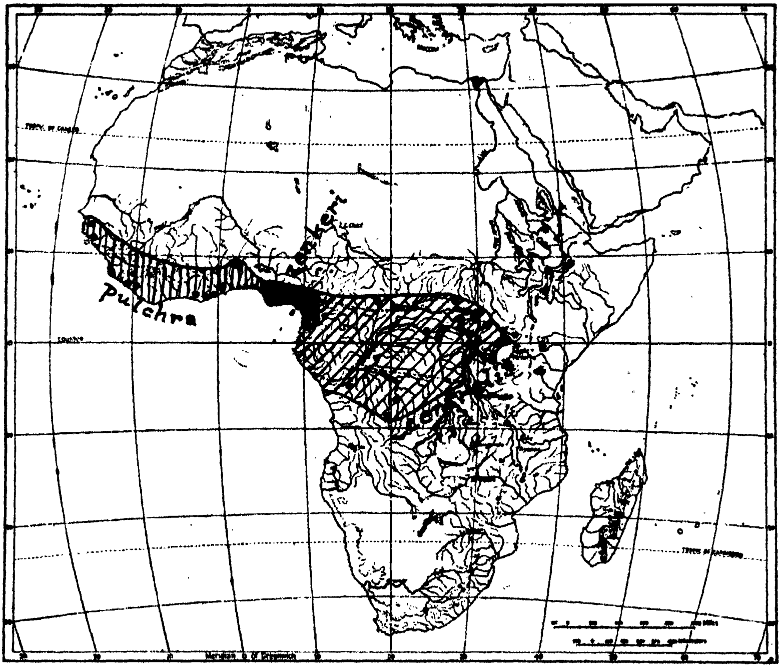

FIG. 5. Distribution of *Sarothrura pulchra*, a small rail frequenting the banks of wooded streams, and extending its range out into the gallery-forests of the Guinean savannas.

They favor reforestation, however, by casting shade sufficient to exclude nearly all grasses. Inasmuch as the natives frequently neglect to cut down all the mature forest trees in their plantations, it is a common thing to find extensive tracts of second-growth woods, overtopped by a sprinkling of true forest trees, yet the birds characteristic of the lower levels in virgin forest will be sparingly represented there. I think I do not exagger-

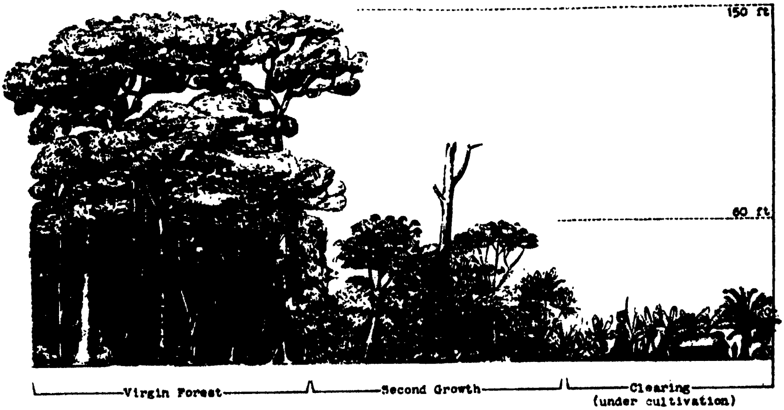

FIG. 6. Diagram to illustrate the succession of forest vegetation after clearing by natives. Note the height of the virgin-forest trees, as compared with the second growth, and the denser lower vegetation in the latter.

ate in estimating the period required for complete reforestation at well-nigh eighty years.

The savannas of Africa vary exceedingly in the abundance of trees and the height of the grass. They occupy the regions where the total annual rainfall is less than 60 inches, or where there is a dry season of two months or more, if not—as in eastern equatorial Africa—two short dry seasons. Many resemblances are seen between the birds of the savannas north and south of the Congo forest; but so often are they specifically different that they seem to indicate more complete segregation in the past, perhaps by the extension of the forest all across the continent. The savannas harbor the horned guinea-fowls (*Numida*), the bustards, the colies, hoopoes, and many other genera of the most characteristic Ethiopian birds.

The avifauna of the deserts is generally more restricted as to species than that of the humid regions, and is characterized especially by sand-grouse, coursers and larks. The distribution of the various forms of ostrich is readily understood if we keep in mind the preference of the group for steppes bordering on the deserts. The four forms commonly recognized in Africa by systematists are characteristic of as many arid regions of the continent, and are kept apart by the more luxuriant vegetation which intervenes.

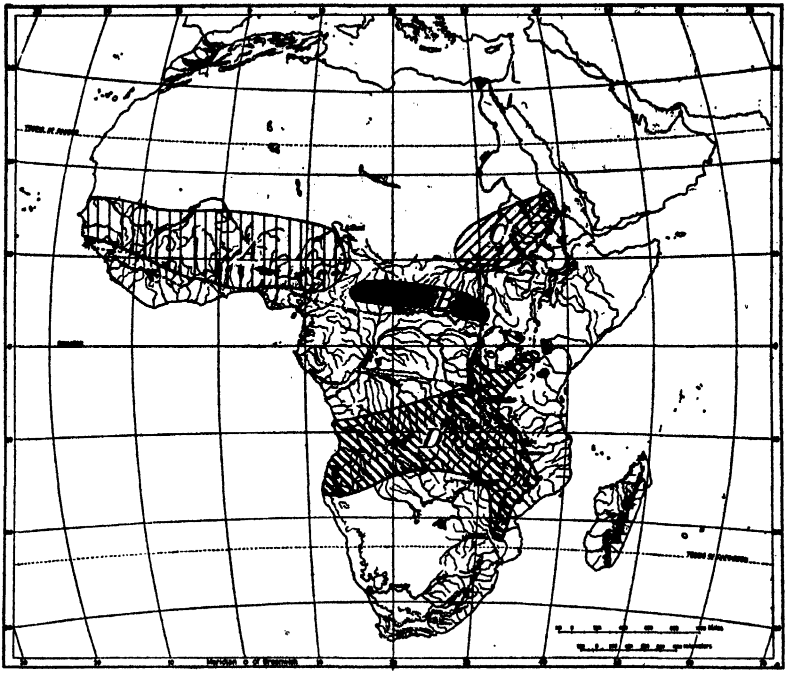

FIG. 7. Distribution of the races of *Steganura aucupum*, the broad-feathered Paradise Whydah. A, *S. a. aucupum;* B, *S. a. interjecta;* C, *S. a. nilotica;* D, *S. a. obtusa*. Such a dispersal is characteristic of many groups of savanna birds, which are segregated by the rain-forest of the Cameroon and Congo.

## ALTITUDINAL LIFE ZONES

Life zones on the African mountains will be found best marked on those peaks which rise within a few degrees of the equator, and therefore are more favored with rains. Between 5,000 and 10,000 feet, on the mountains of the eastern Congo, there is often a complete girdle of mountain- or cloud-forest. This is the habitat of the majority of distinctive mountain birds, which differ specifically in most cases from those of the adjoining lowlands, but are occasionally related to lowland forms in the cooler parts of South Africa.

The upper half of the mountain-forest, in eastern

Africa, is frequently composed of bamboos (*Arundinaria alpina*). Perhaps because of a mingling of vegetation, the bamboo zone is inhabited by much the same birds as the ordinary mountain-forest; so that I am inclined to unite the two floral zones, in so far as birds are concerned, into one subtropical or mountain-forest zone. Above the bamboos, from about 10,000 to 12,500 feet, there is often a zone of tree-heaths, *Erica arborea* on Mt. Ruwenzori, but an *Ericinella* on many of the East African mountains. On some of the Kivu volcanoes there are other large trees at this level, which should correspond to the temperate life zone of the Andes, which Dr. Chapman finds so important in the distribution of South American birds. On the African mountains it is poor in birds, and has almost nothing truly characteristic. I would attribute this to lack of communication with mountains of corresponding height to the north and south, and the small size of the temperate areas themselves.

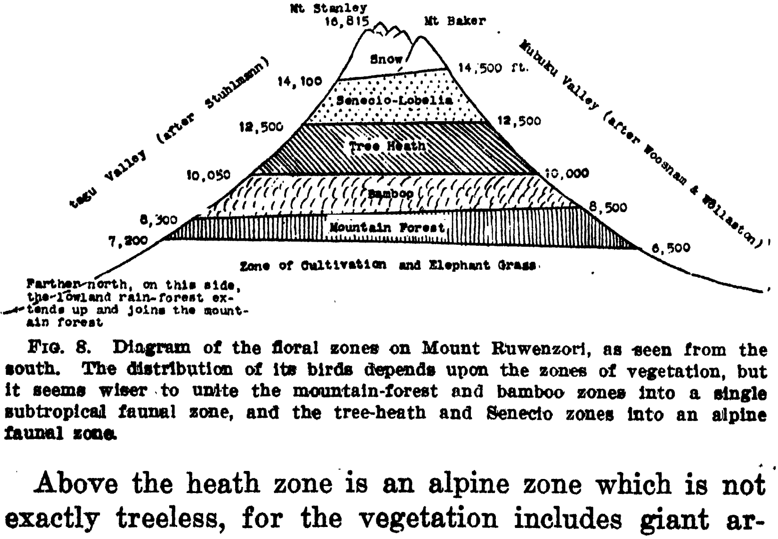
Mt Stanley
16,815
Mt Baker
Snow
14,500 ft.
14,100
Senecio-Lobelia
12,500
12,500
Tree Heath
10,050
10,000
Bamboo
8,300
8,500
Mountain Forest
7,200
6,500
Zone of Cultivation and Elephant Grass
tagu Valley (after Stuhlmann)
Mubuku Valley (after Woosnam & Wollaston)
Farther north, on this side, the lowland rain-forest extends up and joins the mountain forest

FIG. 8. Diagram of the floral zones on Mount Ruwenzori, as seen from the south. The distribution of its birds depends upon the zones of vegetation, but it seems wiser to unite the mountain-forest and bamboo zones into a single subtropical faunal zone, and the tree-heath and Senecio zones into an alpine faunal zone.

Above the heath zone is an alpine zone which is not exactly treeless, for the vegetation includes giant arborescent groundsels and tall lobelias, which dwindle away as the snowline is approached. This cold, inhospitable part of the high mountains has few birds. On Mt. Ruwenzori the British Museum Expedition found only 7 species of birds dwelling in it.[5] To the tall flowering spikes of the lobelias come long-tailed sunbirds, of the species *Nectarinia johnstoni,* which is represented by four races on different mountains of East Africa.

If the heath zone of Ruwenzori be included in the alpine zone, as seems advisable, the whole avifauna will amount to about 15 species of which only four have not been found below the level of the tree-heaths.

## EXPLANATION OF PRESENT MONTANE DISTRIBUTION

The resemblances between birds of the high mountains of Africa extend in a number of cases even to Mt. Cameroon and the peak on the Island of Fernando Po. A trogon of the mountain-forest, *Heterotrogon vittatus,* is found there as well as in East Africa, and shows only

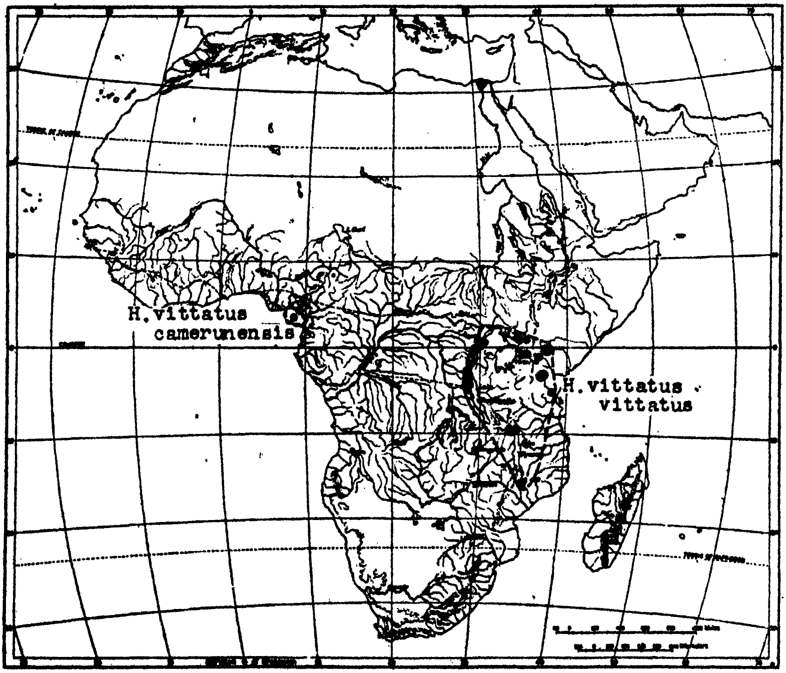

FIG. 9. Distribution of *Heterotrogon vittatus*, a Trogon restricted to mountain-forests. All the central Congo basin, though forested, is too low to harbor it, and this isolation is responsible for the slight differences which have arisen between the eastern and western subspecies.

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[5] R. B. Woosnam, *Trans. Zool. Soc.,* London, 1909–1910, Vol. XIX, pp. 21–23.

a slight subspecific difference. There are parallel similarities in plants, and the botanist Mildbraed,[6] speaking from a thorough acquaintance with field conditions, rejects an explanation based upon chance distribution of seeds by winds or migratory birds. More probably there were changes of topography and climate in the past which permitted extension of the mountain floral zones, thus connecting some of the montane areas now widely separated.

Still more widespread changes in rainfall must be invoked to explain the resemblances between the avian and mammalian faunas of West Africa and the forested parts of the Oriental region. We believe that in Miocene time there was a belt of tropical rain-forest stretching most of the way between India and Africa, where drought now prevails and has long isolated the two forest faunas. Such changes in the vegetation are of more importance for the dispersal of birds than mere land connections would be, across the Red and Mediterranean Seas.

## BIRD MIGRATION AND VEGETATION

In our temperate-zone home, we are accustomed to see birds wander far more widely—as soon as the breeding season is past—than species of the tropics are apt to do. The rigors of our changing seasons necessitate migration. Close to the equator, and especially in a rain-forest, no such incentive exists, and all the small birds are extremely sedentary. But in Africa, as soon as we go a little to the north or south, where an annual dry season parches the countryside, we find seasonal movements of birds by which they tend to adjust themselves to changing conditions of humidity and food-supply. Many move from the drier Sudan, for instance, southward to the savannas closer to the Congo forest, a journey of some few hundred miles. Others cross the humid equatorial belt and find an advantage in the reversed season on the opposite side of the line. Abdim's stork and the pennant-winged nightjar are examples of the latter class.[7] They do not tarry long in crossing the Congo forest, but in East Africa, where there are grassy stretches on the equator, they may stop as well in the intermediate latitudes.

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[6] "Wiss. Erg. Deutsch. Zentr. Afr. Exp. 1907–8," Mecklenburg, 1914, II, p. 689.

The effect of the general type of vegetation is again evident in the migrations of Ethiopian birds. It may also be noted in the winter ranges of many Palæarctic birds which invade Africa annually.

The equatorial forest is a barrier which fixes the

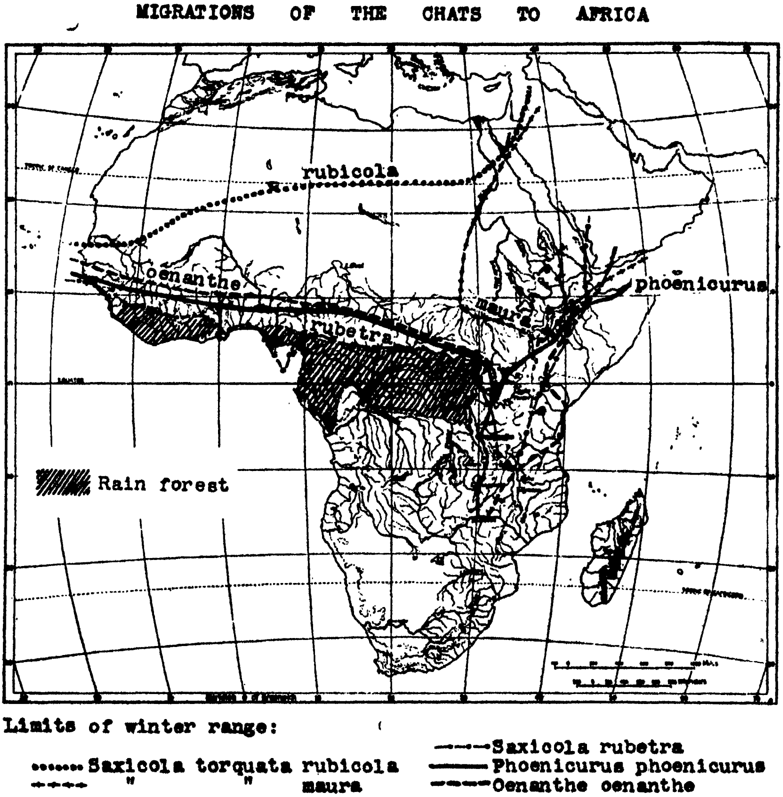

FIG. 10. Migration of the Palæarctic chats to Africa. The lines showing the southern limits of the whinchat, the redstart and the wheatear are clearly fixed by the great lowland rain-forest of western and central Africa, whereas in east Africa, three of the forms go farther south.

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[7] Chapin, James P., *Amer. Mus. Journal*, 1916, pp. 540–545.

southern limit of many species, such as the nightingale, the redstart and the wryneck. Inasmuch as it is broken in East Africa, many species find their way farther south on that side of the continent, some reaching Cape Colony without having to cross the forest belt. Others which extend their migrations to South Africa travel largely along the seacoast (*e.g.*, many shorebirds), or some boldly cross the Congo forest, where they are seen regularly in the clearings (*e.g.*, red-backed shrike, lesser gray shrike, swallow, roller). Such migrants from Eurasia are never seen within the shade of the rain-forest itself.

## AVIFAUNAL MAP OF AFRICA

With Dr. Bequaert's assistance I had divided the territory of the Belgian Congo into eight faunal areas, without counting the further subdivision of the humid montane area into altitudinal life zones. In compiling a complete list of the avifauna of the Congo I discovered that the ranges of the various species and races could be expressed succinctly by reference to these areas, while at the same time they could be readily characterized in general botanical terms.

With this encouragement I tried to extend my avifaunal map to cover the whole continent. My tentative map differs in certain minor points from any of the preceding, though agreeing with them all in the recognition of the faunal importance of "West Africa." This I make one of the two subregions of the Ethiopian region. The avifauna of Madagascar is distinct enough to merit regional separation from continental Africa.

The western fauna owes its distinctness to ecological or climatic conditions, as comparison with the rainfall map of Africa will prove. It is the principal area of more than 60 inches annual rainfall; and I am led to believe—from its dependence on the most fundamental movements in the atmosphere—that such a humid area near the equator is of vast antiquity. Its equable climate and luxuriant vegetation have proved a refuge for

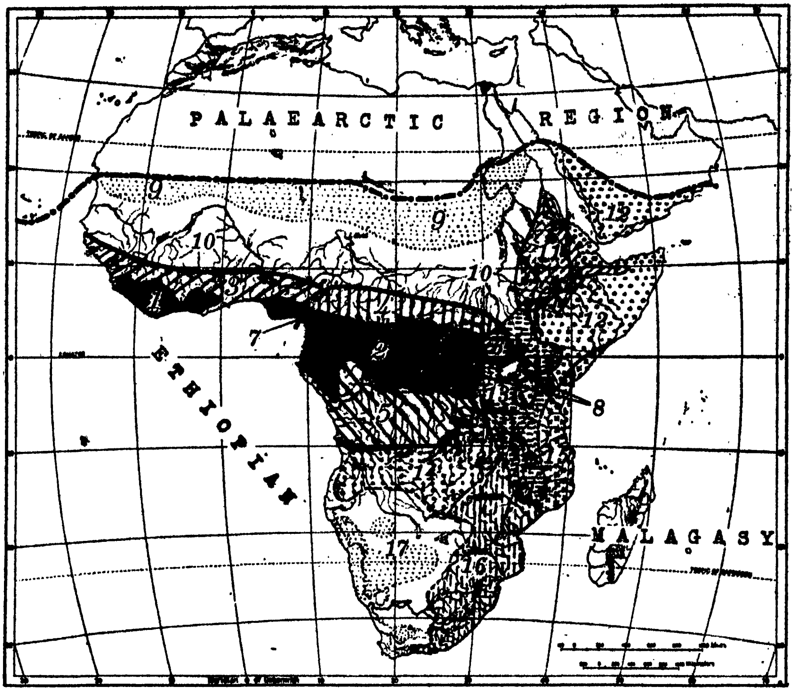

FIG. 11. Avifaunal map of tropical and southern Africa. The Ethiopian region, from which I exclude Madagascar, is divided into two subregions, and these in turn into six provinces composed of seventeen minor districts.

many rather generalized groups of birds, which may have extended farther northward in past geological ages with a more humid climate.

We must not think of the boundary assigned to this subregion as a mountainous ridge offering a barrier to bird travel. Herbert Lang and I spent two years close to the northeastern part of the boundary, in the upper Uelle river district, and found that many species of birds make annual migrations, *en masse,* across this very line. The boundary simply marks the extreme limits of distribution of many members of the forest fauna, the gray parrot, the great blue plantain-eater, and the chimpanzee, because at this point the gallery-forests terminate, due to reduced rainfall during a considerable part of the year. The principal faunal boundary in Africa (for birds and mammals) is ecological, resulting directly from climate.

The influence of topography is more apparent in eastern Africa, because of the effect of elevation upon air-currents and precipitation. Within 5 degrees of the equator elevations over 5,000 or 6,000 feet are very apt to be forest-clad. Yet in 12 degrees south latitude, in the Katanga, at the same altitude the effect is reversed, for the dense savanna woods of lower levels give way to open highland prairies with only occasional gallery-forests along the headwaters of some of the streams. This is attributable partly to the long dry season, of 4 or 5 months, and partly to the poor nature of the soil. Latitude is of more weight in determining humidity than in its effect upon temperature—till we reach the limit of the tropical zone.

Another sharp line of faunal demarcation in Africa is that of the border of the equatorial rain-forest. I mean the line where savannas begin to interrupt the forest. This is the "inner" limit of numbers of savanna forms, even though a few may penetrate to isolated artificial clearings in the forest; and beyond it, too, the forest fauna undergoes rapid diminution, being hidden for the most part in narrow gallery-forests.

Neave[8] has called attention to a marked change in the bird fauna as one rises from the lower Zambesi valley to the higher levels of northern Rhodesia. The change is not due to altitude alone, for many of the birds of northern Rhodesia and the Katanga are found elsewhere at no more than 1,500 feet above sea level.

In East Africa the striking difference between the Tsavo desert district and the highland veldt to the westward has sometimes been spoken of as though due to altitude. This is probably only involved in so far as it affects rainfall.

In South Africa the distinctness of the eastern and western avifaunas is clearly a matter of rainfall and its effect upon the vegetation.[9] North of the equatorial forest we find that there is a similar line of demarcation; but it runs in another direction, from west to east, in a remarkable manner, from Senegal to the Upper Nile. When we follow the long, narrow ranges of many species of birds, from the region of the Gambia across the highlands of Fouta Djalon, down into the low valley of the Niger and up along the Ubangi to the Congo-Nile divide, we can not fail to recognize the unimportance of variations in altitude below 5,000 feet, and the predominant influence of rainfall, as reflected in the vegetation.

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[8] *Geographical Journal*, 1910, Vol. XXXV, pp. 132–144 and map opp. p. 224.

Going a little farther east, we may note that the differences in avifauna and flora between Abyssinia and Somaliland are clearly correlated with rainfall (see map), and only have to do with altitude in so far as this determines the amount of precipitation.

## NATURE OF FAUNAL BOUNDARIES

A word of apology may be necessary for my arbitrary drawing of faunal lines. I know of no better method of calling attention to the differences one would observe in the bird population on going from one part of the continent of Africa to another. I willingly admit that the change is far more gradual than a hard black line would indicate. A broader band of color, fading imperceptibly toward its edges, might carry a truer picture of actual changes. Many species will boldly transgress the limits I have tried seemingly to erect. What I really hold is that there are areas with characteristic complexes or associations of species; and they might be further subdivided, if we cared to, according to more local habitats, depending on the particular haunts of each species—and in this no two are exactly the same.

The travelling ornithologist, as he goes from the Guinean savannas into the rain-forest—for instance—listens to unfamiliar bird voices as he walks along the heavily shaded wood paths. For the first few days practically all of them are strange to his ears. The grass-dwelling birds have been left behind, and a new fauna awaits his investigation.

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[9] The wooded coast of Natal is perhaps worthy of separation as another district, making three in all, for South Africa.

## SUMMARY

The general conclusion to be drawn from my map is that although temperature may be a distributional factor of weight, it acts most visibly along certain critical lines, as that, for instance, where occasional frosts first occur. Such a line may be a rough boundary for the tropical life zone, altitudinally as well as on the north and south. Other similar lines are found as the subarctic region is reached, and on mountains, where trees disappear.

Within the limits of the tropical zone, temperature alone has no further effect on distribution; humidity now becomes the predominating factor. Its effect upon bird distribution is produced through the development or the paucity of vegetation, the relation between plant associations and their bird inhabitants being particularly close in the African tropics. Avifaunal lines of demarcation are never more sharply defined than the changes in composition and habit of the vegetation. A difference in plant associations may also serve as an isolating factor, just as often as altitude. More than likely, the isolation by altitude, indeed, is again secured through changes of the montane plant-formations.

### *Subdivisions of the Ethiopian Region*

I. West African Subregion.
  *A*. Guinean Forest Province.
    1. Upper Guinea Forest District.
    2. Lower Guinea Forest District.
  *B*. Guinean Savanna Province.
    3. Upper Guinea Savanna District.
    4. Ubangi Savanna District.
    5. Southern Congo Savanna District.
    6. Uganda-Unyoro Savanna District.
II. East and South African Subregion.
  *C*. Humid Montane Province.
    7. Cameroon Montane District.
    8. Eastern Montane District.
  *D*. Sudanese Province.
    9. Sudanese Arid District.
    10. Sudanese Savanna District.

*E.* Northeast African Province.
  11. Abyssinian Highland District.
  12. Somali Arid District (incl. S. Arabia).
*F.* Eastern and Southern Province.
  13. East African Highland District.
  14. Angolan Highland District.
  15. East African Lowland District.
  16. Southeast Veldt District.
  17. Southwest Arid District.

# REPTILES IN THE EAST AND WEST INDIES—AND SOME DIGRESSION

T. BARBOUR

AGASSIZ MUSEUM, HARVARD UNIVERSITY

THE more nearly complete knowledge of the fauna of the earth which has resulted from the intensive collecting of the last few years has inevitably forced changes in zoogeographic concepts which were previously held. Wallace's line has gone and the North American Life Zones, so favorably discussed by writers only a few years ago, are now definable in a small way only. Thus, as Dunn has put it, where zonal lines coincide with physiographic barriers there is a noticeable change of fauna within a few miles and the result is a visible and definable limit. Lutz's paper on "Geographic Averages" served some useful purpose in emphasizing the unsatisfactory state of our terminology for faunal divisions within the greater land masses. We can not see, however, that he has offered a happy issue out of this affliction. None of the areas previously defined has really described the distribution of more than a very few forms and these only in vague terms. Dunn has made a suggestion pregnant with possibilities of future usefulness, viz., to use the "New Geography" and he has already used the "Physiographic Divisions of the United States," prepared by Fenneman, with real ease and comfort. When such divisions are defined for the other continents, then most, if not essentially all, of our present difficulties will cease to exist. In the areas which I have chosen to remark upon there are no zones to be named, for the East and West Indies are made up of broken lines of islands and the adjacent elements of each chain differ in their faunas one from the other in moderate degree. In the East Indies there is no Wallace's line, no Weber's line and no sharp boundary of any sort which defines the ranges of more than a few species. Java once was thought to have had a separate connection with the Malay Peninsula independent of that which Sumatra and Borneo had, but more skillful collecting in this island has changed this concept and now we know that Java had just the fauna to which its geographic history and position entitles it; namely, a purely Malayan fauna rather depauperate in proportion to its distance from the mainland and its lesser area. Other factors such as climate, rainfall and accessibility, being equal, the larger the island the greater the number of species to be found there and *vice versa.* In the East Indies in proportion as obviously continental types grow fewer, others derived from Australia make their appearance, so that in Lombok there are many species of Malay origin and a few of Australian, while in Ceram or Halmahera the exact reverse is true. Thus the whole central portion of Insulindia is in reality a great transition zone. What makes this contrast striking is the fact that Asiatic and Australian species are so different in facies and are so easily recognized. The many survivors of the early types which now we call Australian species have filtered back toward the mainland as various foldings and thrusts up and down have brought various islands into temporary union for greater or lesser periods of time. That the Australian types in Celebes, for instance, are reentrants and not survivors is reasonably certain, we believe. Celebes, nevertheless, has an obviously "continental" fauna by all tests and still is not a "continental" island oceanographically and the proportion of Australian species is small but conspicuous. The condition seen in Celebes is the strongest single argument against the tenets of those who maintain that flotsam and jetsam are sufficient to account for the population of these islands. We have discussed fortuitous dispersal so fully elsewhere that there is no occasion to expand on this theme at present.

How, then, after these digressions, does the distribution of East and West Indian reptiles compare? Are conditions similar? Similar in part they certainly are, geographically. In both cases a long series of tropical islands stretch out to form a giant set of stepping stones between two continents. But in the case of Australia we deal with an island, very long isolated, while South America, greatly modified from ancient Gondwana land, is connected by Panama with Central America. South American species are far less conspicuously different from Central American than Australian are from Asiatic, for there has been less isolation to permit of change.

In the East the mainland agamids wane and but few reach Papua while the Australian skinks abound in Papua and the Moluccas and dwindle in numbers in the greater Sunda Isles. Respecting the East Indies we instinctively illustrate degree of difference by citing the distribution of *families,* whereas in the West Indies we must discuss *genera.* Thus the Central American Bufos reach out through Cuba and Haiti to little Virgin Gorda. Gymnophthalmus, Centropyx and Scolecosaurus push into the Lesser Antilles from the Guianas. But the greater part of the essentially Antillean genera range throughout the whole chain and are found on every island, islet or even rock which can support life, and this most significant homogeneity of the fauna is here the paramount argument against fortuitous dispersal. The fact that a single genus ranges all through the islands, however, is no certain proof of derivation from one mainland source only, for in the case of Ameiva and Anolis, for example, it is possible to identify groups of species within the genus, inhabiting adjacent islands, and which have come in from the opposite ends of the island chain.

A moment to compare the facies of the faunas is well spent, too. Over much of Indonesia the skinks are dominant, successful types, arboreal, terrestrial, subterranean—even semi-aquatic. In the West Indies they are on the verge of complete disappearance. Species occur on many islands but all are on the verge of extinction. In the East Indies the Agamidæ, while conspicuous in the greater Sunda group, are not preeminently the dominant family anywhere. In the West Indies the cognate family of Iguanidæ are enormously successful. Anoles in Jamaica swarm as no lizard swarms anywhere except Lygosomas in Papua. The bold semipredaceous Varanids of the East Indies have no counterparts in the West, their place being taken by the Ameivas belonging to a family (Teiidæ) really cognate with the old world Lacertidæ, a family which has almost no hold in Eastern Asia.

Such illustrations might be multiplied but to no useful purpose.

The East Indies illustrate, on a vast scale, not only in space but in geologic time, what the Antilles recapitulate.

We may sum up by saying that distributional conditions in the West Indies are the counterpart of those in the East but differ in being in all respects lesser in degree. Their fauna occupies less area, has existed in isolation for a far shorter period of geologic time and therefore shows less taxonomic differentiation. The points of similarity are: the mixed fauna derived from two opposite sources, the relatively homogeneous fauna of contiguous islands and groups of islands, showing that the great bulk of the species involved have been derived as a result of changes of the relation of land and sea level, which have put the islands into transitory union. In both areas the waif species which have been carried about fortuitously, and there are inevitably such, can be easily recognized.

# THE GEOGRAPHICAL DISTRIBUTION OF AMPHIBIANS

DR. E. R. DUNN

SMITH COLLEGE

IN presenting for your consideration the geographical distribution of Amphibians I have been guided in my choice of examples by their bearing on two of the more recent theories, namely, the theory of dispersal as set forth by W. D. Matthew in 1915 in his "Climate and Evolution," and the "Age and Area" hypothesis of J. C. Willis as proposed in papers from 1906 on, and restated in full in 1921.

The theses of Matthew which shall hereinafter be examined are stated by himself as follows:

1. Secular climatic change has been an important factor in the evolution of land vertebrates and the principal known cause of their present distribution.
2. The principal lines of migration in later geological epochs have been radial from Holarctic centers of dispersal.
3. The geographic changes required to explain the present distribution of land vertebrates are not extensive and for the most part do not affect the permanence of the oceans as defined by the continental shelf.
4. The theories of alternations of moist and uniform with arid and zonal climates, as elaborated by Chamberlin, are in exact accord with the course of evolution of land vertebrates, when interpreted with due allowance for the probable gaps in the record.
5. The numerous hypothetical land bridges in temperate, tropical, and southern regions, connecting continents now separated by deep oceans, which have been advocated by various authors, are improbable and unnecessary to explain geographic distribution. On the contrary, the known facts point distinctly to a general permanency of continental outlines during the later epochs of geologic time, provided that due allowance be made for the known or probable gaps in our knowledge.
6. Whatever agencies may be assigned as the cause of evolution of a race, it should be at first more progressive at its point of original dispersal, and it will continue this progress at that point in response to whatever stimulus caused it and spread out in successive waves of migration, each wave a stage higher than the previous one. At any

one time, therefore, the most advanced stages should be nearest the center of dispersal, the most conservative stages farthest from it.

It seems evident that no matter where the primitive or the advanced forms of a group are found the center of dispersal of that group should be the geometric center of the group range; or better, the geographic center, by which is meant the center of available migration routes. This idea is not definitely stated by Matthew, but it underlies his whole conception of radial migration from Holarctic centers, for granted continental permanence, the southern continents are radial to the northern land mass.

Let us now examine the distribution of Amphibian groups.

The blind, burrowing Cœcilians are Tropicopolitan. The geographic center of the Tropics is the northern land mass. The Cœcilians have reached their present ranges either by a process of retreat from a more continuous northern range, or else, by a perfectly gratuitous assumption of tremendous changes in the earth's surface, they have crossed from Africa to South America, and from Africa to India.

The *Salientia* have been examined recently by Noble, and I follow his classification.

The *Pipidæ* form a primitive family and they are restricted to South Africa and to northern South America. This distribution may be contrasted with that of a modern family, the *Ranidæ,* which occupies the whole northern hemisphere, as well as Africa, India, Malaysia and Papua, but barely reaches Australia and South America. These two families offer perfect examples of the distribution of a primitive and of a modern group as postulated by Matthew.

Several families of *Salientia,* while world-wide or nearly so, are mainly developed in the southern continents. Such are the *Bufonidæ,* the *Hylidæ,* and the *Brevicipitidæ.* The distribution of these groups has often been held to indicate former direct connection between the southern continents, an hypothesis involving vast changes in continental outline. But no genera of Bufonids are common to South America and to Australia, none to Africa and to Australia, *Bufo* alone is common to Africa and to South America, while two genera besides *Bufo* are common to Africa and to Indo-Malaysia. The best explanation here is dispersal from a northern center. Similarly, *Hyla* is the only genus of *Hylidæ* common to South America and to any of the other southern continents, and it, as does *Bufo*, has a wide northern range. Among the *Brevicipitidæ* one genus is found both in Africa and in the East Indies, none of the other genera being common to any two of the southern regions. These two cases, like that of the *Bufonidæ,* may be explained by Matthew's theory, which involves connections only in the north between the northern continents, and hence calls for no great changes in continents or in oceans.

The *Pelobatidæ* are mainly developed in the Indo-Malay region, but some forms are found in Europe and in North America. This is surely a dispersal from a northern center, the peculiarity being that while the *Pelobatidæ* are considered a rather primitive family, they have not spread so far to the south as have the less primitive Bufonids and Hylids.

A similar anomaly, from the standpoint of Matthew's hypothesis, is presented by the most primitive family of Salientians, the *Discoglossidæ* (which alone possess ribs). Their range extends, with some breaks, across Eurasia, two species are found in New Zealand, and one in the State of Washington. This discontinuity gives evidence of vast former range and of great antiquity. No other Amphibian has reached New Zealand. But there is no lack of forms in the northern land mass.

Furthermore a modern family, the *Brachycephalidæ,* is confined to South and Middle America, and supposed to have arisen there from Bufonids.

It is clear that so far Matthew's theory is a fair means of accounting for the discontinuous distribution of southern groups; but the primitive groups are not always at the periphery; nor is it impossible for new groups to arise in the South.

The distribution of Salamanders has little bearing on the problem of northern origin, for they are almost confined to the north. One case, however, has been used as a basis for a land bridge between southern Europe and the West Indies. I allude to the supposed relationship between the Plethodont salamanders of Central America, Haiti and Italy. There is actually no close relationship between the animals of Italy and those of Central America. The Haitian salamander is either mythical or related to a Central American form. The most startling zoogeographical discovery made in the United States since Stejneger announced the finding of a Discoglossoid toad in the Olympic mountains was that of *Spelerpes platycephalus* in the Yosemite by Camp. This animal is almost identical with the Plethodont of Sardinia. So link by link the chain of argument whereby salamander distribution supported Archatlantis is broken.

The distribution of the genus *Triturus* of the family *Salamandridæ* affords an interesting example of dispersal as postulated by Matthew. This group occurs throughout Eurasia. Three species in the eastern United States are closely related to some forms of Europe, and the form of the Pacific Coast is allied to a Chinese species. The center of the group range is Europe, and judging from the relationships of the American species, this is also the center of dispersal. But besides this the group has characters whereby the primitive and specialized members can be distinguished. Sexual dimorphism can not be considered primitive, while a bony temporal arch may well be an archaic character. If we consider the distribution of these two characters in *Triturus,* the extreme sexual dimorphism is found in

Europe, dying away in eastern North America, and in Asia and western North America. The bony temporal arch is least developed in Europe, most in Asia and in America. Thus the primitive members are found at the periphery and the specialized members at the center which had been previously determined by two other lines of evidence.

The results just obtained are supported by the distribution of two still more primitve genera of the same group, *Pleurodeles* and *Tylototriton.* These range to the south of *Triturus; Pleurodeles* in Spain and in Africa as far south as French Guinea on the west coast, and *Tylototriton* in the Eastern Himalayas, Yunnan and Burma, and the Riu Kiu Islands.

The largest family of salamanders, the *Plethodontidæ,* has in many ways the most interesting distribution. Although probably the most modern group of Urodeles, it is of no mean age, as is attested by *Ensatina platensis* of Uruguay which is almost indistinguishable from *Ensatina croceater* of California. It is hard to believe that this genus can be of less than Miocene age. *Hydromantes platycephalus* of California, which has as its very close ally *Hydromantes genei* of Sardinia, affords another suggestion as to the antiquity of Plethodont genera.

The family is an eminently natural group, all lungless, mainly developed in North America, with four species in South America and two in Europe.

Lunglessness in salamanders seems theoretically and actually correlated with mountain brook life. Theoretically because the lungs of salamanders are largely hydrostatic in function, and because such hydrostatic organs would put the animal at a disadvantage in a swift current where the mode of progression is crawling on the bottom. Actually because a Hynobiid, an Ambystomid, and six Salamandrids are independently undergoing lung reduction, and are all mountain brook animals. It seems reasonable to conclude that the family

*Plethodontidæ* originated (took on its family characters) in a mountain region.

The problem before us is to determine this region of origin, the center of dispersal, which must have been mountainous. The geometrical or geographical center of the group range is the eastern United States. In the eastern United States and there only are found at present: The most primitive forms; all the groups of the family; all the forms now living in mountain brooks.

The original mountain-brook habitat has been largely abandoned, and many members of the family are now terrestrial. Such terrestrial forms, all lungless, are found throughout the range of the family. The assumption of this terrestrial mode of life was a necessary preliminary to migration out from a mountain region.

All this leads to one conclusion: that the *Plethodontidæ* originated in and have dispersed from the mountains of the eastern United States, in a word from Appalachia. We have arrived at this result irrespective of the fact that the primitive forms are at present restricted to Appalachia, by arguments from the center of the range, from the origin in mountain brooks (the anatomy), and from the present position of the mountain-brook forms (the ecology). Why does this result differ from Matthew's theory? Because Appalachia is an old and a conservative region, while the radial migration of his hypothesis is caused by changing conditions at the center. On the contrary, in Appalachia there have been mountains since the close of the Paleozoic; a climate now the most humid in the East; formerly not less humid, since the uplifting of three mountain ranges to the west, and the filling in of the Mississippi Embayment can only have decreased the rainfall. Therefore, in this most stable of regions there has been no such cyclic swing of change as has sent out incessantly higher and higher types from the northern hemisphere.

To sum up: The distribution of Amphibians offers as a critique to Matthew's "Climate and Evolution" the following:

All amphibian distribution can be explained without recourse to land bridges save connections in the north between the northern land masses.

The primitive forms are not always at the periphery, although they are often found there, but may be found at the center.

The center of dispersal is best determined by the geographic center of the group range.

One family, modern and progressive, seems to have arisen fairly recently in South America.

The Age and Area hypothesis of Willis maintains that the older a genus the wider will be its range, and the greater its number of species, also that the older a species the wider its range.

From a practical standpoint the use of range to determine age is open to several objections:

There is no evidence of the use of any data from comparative morphology, or from paleontology, or from phylogeny. These, when correct, should support or undermine his theory.

Even if generally true, so long as there are any exceptions each case must be decided on its own merits and therefore size of range or number of species can never be a complete criterion for age.

No allowance is made for extinction of old groups which must be of as common occurrence as formation of new ones. This is the main objection. A genus both at its inception and at its extinction should contain one species. This Willis disregards, with the result that mature groups are called "old," and both young and old groups are called "young."

The following cases of Salamander distribution, in which relative age of groups is determined by comparative morphology and phylogeny, will serve to illustrate Age and Area.

The family *Hynobiidæ* contains five genera. The most primitive of these, *Hynobius,* contains fifteen species and has an enormous range, throughout northern Asia. It has given rise to four more specialized genera, three of them monotypic, and one with two species. These four daughter genera have very restricted ranges, three (and probably all) within the range of the parent genus.

Here evidently the oldest genus has the widest range and the greatest number of species. But the accepted ages of the groups do not rest upon size of range or upon number of species. They rest upon the comparative morphology of the forms.

In the *Plethodontidæ* the most primitive genus is *Gyrinophilus* with two species and a moderate range. The most specialized is *Leurognathus* with one species and a very restricted range. The largest genus *Œdipus* is much less primitive than *Gyrinophilus* and hence younger, but as it has given rise to one daughter genus it is neither the oldest nor the youngest, and should properly be considered mature and successful.

Willis has presented a theory which is sometimes, as in the case of the *Hynobiidæ,* supported by the facts; and sometimes, as in the case of the *Plethodontidæ,* both supported and contradicted. Age can only be determined by careful phylogenetic work, and attempts to determine it by computation are excellent examples of the use of statistics in support of conclusions to which they are irrelevant.

Thus the facts of distribution in one small group afford support to both sides of two much contested arguments. To paraphrase Wilde, "The only general rule is that there is no general rule."

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# FAMILY RESEMBLANCES AMONG AMERICAN MEN OF SCIENCE

DR. DEAN R. BRIMHALL

SECRETARY OF THE PSYCHOLOGICAL CORPORATION

## III. THE INFLUENCE OF THE NEARNESS OF KINSHIP

IT would seem reasonable to suppose that the nearer men are in "blood relationship," the greater would be the resemblance in performance. Brothers are more nearly related than father and son; do the brothers of distinguished men of science outnumber the sons, or the fathers, or the uncles? It has been shown that brothers resemble each other in performance in science more than cousins. In proportion to their numbers about five times as many brothers of starred men obtain positions in the starred group as cousins. Is there an increasing number of distinguished relatives with increasing closeness of relationship? The results recorded in this chapter show that there is.

### DEGREES OF KINSHIP

If for no other reason than that reproduction of human beings is bisexual it is reasonable to suppose that brothers are more nearly related than cousins or than grandsons and grandparents. The zygotes from which brothers grow are each the result of a combination of individual cells (gametes) from two different groups of cells. If we assume that the germ cells from the male vary about a common point which in turn varies from the common point of the species, the chances are that the offspring will vary from the mid-measure of the species in the direction of the variation of the parent. If we assume that the parent's qualities give a clue to the kind of germ cells he carries, that is, if we assume that a man of genius carries germ cells which vary as a group from the germ cells of the species and that the average of these variable cells of the individual closely resembles the zygote from which the man developed, the chances are certainly remote that the maternal side will furnish a gamete for the union that will maintain the zygotic resemblance.

The problem of apparent blending in resemblance as in the case of pigmentation of offspring of negroes and whites and of Mendelian or alternative inheritance in the case of eye color are beyond the scope of this study. Biologists do not seem to be agreed on the decree to which one may generalize, as the following quotation would seem to show:

> It seems best, accordingly, to attempt neither with Galton to generalize all inheritance as blending nor with Johannsen to treat all inheritance as alternative, but frankly to recognize the existence of two categories of cases distinct in their inheritance behavior.[1]

Whatever the method, blending or alternative or both without a very exact assortive mating the union of two gametes will produce an individual that is as a matter of chance less likely to resemble either parent than if the individual developed asexually. This factor, then, would tend to decrease the resemblance of near relatives to a degree that would vary as the number of matings is involved. If the gametes of any individual actually vary about an average that is approximated by the zygote from which the individual who carries them grew, it is likely that of two brothers one carries a group of germ cells superior, on the average, to the germ cells of the other. It is conceivable that the "inferior" of the two carries a group of cells superior to the "superior" brother. Speculations of this sort belong to workers more familiar with experimental genetics. They are given as suggestions of the complications of the apparently simple problem of determining the relative influence of the different ancestors.

## DISTINGUISHED RELATIVES IN EACH DEGREE OF KINSHIP

Whatever the values of the intervals between the different relationships may be, the following order is assumed to be valid in the sense that closeness varies according to the following order:

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[1] W. E. Castle, "Genetics and Eugenics," 1916, p. 218.

(1) Brother and sister
(2) Father, mother, son and daughter
(3) Uncle, aunt, niece and nephew
(4) Grandparent
(5) Cousin

The details concerning the number of relatives of distinction in each specific relationship are given in table four but they are repeated as part of table six to facilitate comparison. It will be noted that the specific kinships recorded in this table are arranged in the assumed order of nearness.

TABLE VI

| | Detailed Grouping | | Totals of Each in Course Grouping |
|---|---|---|---|
| Brothers and sisters | B | 146 | |
| | Si | 13 | 159 |
| Sons, daughters, fathers and mothers | S | 18 | |
| | D | 1 | |
| | F | 78 | |
| | M | 3 | 100 |
| Uncles, aunts, nieces and nephews | FB | 33 | |
| | FSi | 4 | |
| | MB | 31 | |
| | MSi | | |
| | BS | 6 | |
| | BD | 3 | |
| | SiS | 3 | |
| | SiD | | 80 |
| Grandparents | FF | 17 | |
| | FM | 1 | |
| | MF | 35 | |
| | MM | 1 | 54 |
| First cousins | FBS | 45 | |
| | FBD | | |
| | FSiS | 15 | |
| | FSiD | 2 | |
| | MBS | 20 | |
| | MBD | 1 | |
| | MSIS | 18 | |
| | MSiD | 4 | 105 |
| Total | Total | 498 | 498 |

It is obvious that the raw totals in the course grouping are without significance except as they give a sort of bird's-eye view of the situation. It can be seen at a glance that eight specific first cousin relationships do not furnish as many relatives of distinction as the two relationships of brother and sister. The comparison is no less striking if only the males are considered. In this comparison there are 146 brothers and 98 first cousins. These two groups happen to be rather directly comparable, the factors making for inclusion of those of the one group about equalling the factors making for inclusion of members of the other. But the other relationships and the source of those included make certain considerations of importance necessary. Two of these considerations are (1) the number of persons in each specific relationship, that is, the number of brothers, the number of sisters, the number of mothers, fathers, the number of individuals in each one of the eight first cousin kinships and so on; (2) the equality of certain of the chance factors determining inclusion for the different groups in any one of the handbooks by which distinction is measured.

In direct ancestry the number in each degree of kinship is obvious. A man has in each and every specific ancestral relationship one relative. He has one father, one mother, one FF, one MF, one FFF, and so on *ad infinitum*. Furthermore, each of the individuals in the direct ancestry reaches an adult age, if ability to reproduce is a measure of maturity. Certainly, all do not reach the average age at which men obtain a place in a biographical handbook. Age and number of offspring have a positive correlation, however.

In the collateral ancestry and in descendants the number does not lend itself so easily to deduction. In a stationary population the average number of fertile relatives in each specific kinship would equal the number of ancestors in each specific relationship, which has been shown to be one.[2] Furthermore, Galton, in the work just cited, proposes: "that the number of fertile individuals is not grossly different to that of those who live long enough to have an opportunity of distinguishing themselves."

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[2] Noteworthy families, Galton and Schuster, p. 33.

Galton's study dealt with the families of members of the Royal Society living in 1904. The data concerning the near relatives of 100 of these men were collected and the findings on the number in each specific relationship are given in the table below (see Table VII).[3]

TABLE VII

| Kinship (Males) | Number | Kinship (Females) | Number |
|---|---|---|---|
| Brothers | 206 | Sisters | 207 |
| Uncles (FB) | 228 | Aunts (Fsi) | 207 |
| Uncles (MB) | 219 | Aunts (MSi) | 238 |
| Cousins (FBS) | 263 | Aunts (FBD) | 302 |
| Cousins (FSiS) | 184 | Aunts (FSiD) | 208 |
| Cousins (MBS) | 236 | Aunts (MBD) | 266 |
| Cousins (MSiS) | 237 | Aunts (MSiD) | 246 |
| Totals | 1575 | | 1674 |
| Average per man | 2.25 | | 2.39 |

For our purposes these data are important in showing that whatever the number of relatives in specific degrees of relationship may be, it is approximately the same for those relationships other than direct ancestry. Direct ancestry can not include infertile people; collateral ancestry and direct descendants furnish the infertile part of the population, that is, those who die before maturity and those who reach maturity but do not reproduce. If the above is a correct analysis, it would seem proper to compare the direct ancestors, coming from a stationary population, with each other, allowing only for the relative number in each degree. Such an arrangement would result in an order beginning with the father-mother relationship of two and would increase by doubling in each successive degree of remoteness, as follows:

| | |
|---|---|
| **Father–mother** | 2 |
| **Grandparent** | 4 |
| **Great-grandparents, etc.** | 8 |

[3] *Ibid.*, p. 30.

The progression for the collaterals and descendants, beginning with the brothers, would be:

| | |
|---|---|
| Brother–sister | $2 + 2x$[4] |
| Son–daughter | $2 + 2x$ |
| Uncle–aunt | $4 + 2x$ |
| First cousin | $8 + 8x$ |

Owing to the completeness of the reports by the men of science it is possible to determine, that for the brothers and sisters X is not smaller than .22. For 1,000 men of science the computations showed 1,264 brothers and 1,180 sisters, *i.e.*, 2,440 siblings, living at the time the replies to the questionnaire were sent in. This means that there were 2.44 siblings per man in these relationships, or approximately 1.26 per brother relationship and 1.18 per sister relationship. It seems reasonable to suppose that these figures are too high. The death rate among the professional classes is said to be lower than among the generality, but such a low death rate as these figures would indicate is probably incorrect. If a comparison were to be made between the direct ancestors and the collaterals in which the unit value in the former be called one and the unit value in the latter be called 1.22, it would seem that the validity would be greater than if the unit value were considered 1 in all cases as Galton proposes.

## NUMBER OF DISTINGUISHED RELATIVES IN EACH DEGREE OF KINSHIP

It now becomes necessary to examine more carefully the method of determining distinction, since three handbooks, covering somewhat different periods, and with different selective standards, were used.

Both editions of "American Men of Science," that is, the editions of 1903 and 1910, were consulted, and biographies found in either were counted. Those found in the original edition of Appleton's "Cyclopedia," published in 1887–8, together with the appendix of 1890 and all ten volumes of "Who's Who in America" covering the period from 1910 to 1918 were also included. The first edition of "American Men of Science" contains more than 4,000 men of science, of entire North America, the second edition of 1887-88 of Appleon's Cyclopedia of American Biography contains "above 15,000 prominent native and adopted citizens of the United States, including living persons, from the earliest settlement of the country." In the appendix of 1890-00 "will be found nearly 2,000 notices of Americans who won renown in the war with Spain . . . and of persons of the New World who have become prominent in the peaceful activities of life during the decade" between the appearance of the two publications. The ten volumes of "Who's Who in America" contain 36,915 biographical sketches. The first volume contains 8,602 biographies, while volume 10 has 22,968. It is evident that the three publications have varying standards of selection, and it becomes necessary to get some statement of the degree of fineness of selection represented by each.

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[4] X equalling the number that must be added to one to make up for those who die before reaching maturity or who do not reproduce though they reach maturity.

Appleton's "Cyclopedia" covers a period of nearly four hundred years. The small population in the early periods with which it is concerned, and the probability that the later periods, namely, the periods during which the grandparents and older fathers of the men of science might have been included, are unduly favored has led the writer to assume a fineness of selection of double that of "Who's Who in America," or one in 2,500 of the generality. Whether this guess has any great validity does not greatly affect the major part of the results in this chapter. If the reader has reason to doubt the proportion, the comparisons of the grandparents with the other relatives may be ignored. The grandparents are the only important group affected.

The ten volumes of "Who's Who in America" that were used are reported by the editors (see preface of Vol. 10, 1918-19) to contain 36,915 individual biographies for a period covering nearly 20 years. The varying numbers in the different volumes do not correspond in relative size with the changes in population. The population of the United States in 1900 was 75,000,000, in 1910 it was 92,0000,000, in 1920, if the growth followed the curve of growth during the two preceding decades, 110,000,000. The ratio of 8,602 to 75,000,000 is approximately 1 to 8,700. The ratio of 22,968 to 92,000,000 is 1 to 5,243 for the generality. For 1912–13, it is 18,794 to 94,000,000 estimated or 1 to 5,000 of the total population. Since the majority of the biographies of relatives found in "Who's Who in America" are in the later editions, and since the editors omit mention in each succeeding edition of a considerable number of those in a previous edition, the ratio of 1 to 5,000 will be used.

Of the 498 relatives of distinction there are 33 whose biographies are found in "American Men of Science" exclusively, and, owing to the specialized requirements for inclusion, this book is used only for special cases described below. No special consideration is given, therefore, to the fineness of selection, other than that used in part II.

Table VIII gives what seems to be the most important facts concerning the distribution of relatives of distinction in the various relationships. Some of the reasons for limiting the comparisons to the specific relationships have been given and certain justifications for including the fathers, who are direct ancestors, with the others who are collateral relatives have been implied. The full number of fathers who reached the required average age is probably less than the number of brothers found to have reached this age. However, practically all fathers had had full opportunity to become distinguished, whereas not all brothers and first cousins had. On the other hand, the fathers who died before the first issue of "Who's Who in America" had less opportunity to be included in other than Appleton's "Cyclopedia." The uncles present somewhat the same problem as the fathers, except for number.

The sons, daughters, nieces and nephews are excluded from this comparison by age. Diminishing birthrate also makes such direct comparison of the younger members with the older impossible.

## TABLE VIII

### Distribution of Distinguished Relatives According to Degree of Kinship

| Relationship | Distinguished Relatives (1) | Number of Relatives Reduced to Comparable Ratios (2) | Facts of Column Two Expressed in Per Cent. (3) |
|---|---|---|---|
| Brothers and sisters.. | 140 | 140 | 50.5 |
| Fathers and mothers. | 78 | 78 | 28.2 |
| Uncles and aunts.... | 68 | 34 | 12.3 |
| First cousins........ | 100 | 25 | 9.0 |
| Total. | 386 | 277 | 100.0 |
| | *Distribution of Males* | | |
| Brothers. | 127 | 127 | 49.4 |
| Fathers.. | 75 | 75 | 29.1 |
| Uncles.. | 64 | 32 | 12.5 |
| Cousins.. | 93 | 23 | 9.0 |
| Total. | 159 | 257 | 100.0 |
| | *Distribution of Females* | | |
| Sisters... | 13 | 13 | 65.8 |
| Mothers. | 3 | 3 | 15.2 |
| Aunts... | 4 | 2 | 10.1 |
| Cousins. | 7 | 1.75 | 9.0 |
| Total. | 27 | 19.75 | 100.0 |
| | *Distribution of Males with Grandfathers Included* | | |
| Brothers...... | 127 | 127 | 44.9 |
| Fathers........ | 75 | 75 | 26.5 |
| Uncles......... | 64 | 32 | 11.3 |
| Grandfathers.. | 52 | 26 | 9.2 |
| Cousins (male). | 93 | 23 | 8.1 |
| Total. | 411 | 283 | 100.00 |

Since all of the 52 distinguished grandfathers were recorded in Appleton's "Cyclopedia" and since it was assumed that the fineness of selection of that handbook was greater than the other handbooks, it seems probable that the per cent. column is invalid in that relationship. There remain the more valid differences in the brother and cousin relationship and in the father-uncle groups.

According to the figures in Table VIII, a person from the brother-sister relationship is almost twice as likely to be distinguished as one from the father-mother relationship, four times as likely as one from the uncle-aunt group and between five and six times as likely as one from the cousin group. The females are too few in number to make such comparisons valid for them. They are given in the separate section of Table VIII because the reader may be interested in their distribution in spite of the small number. Probably the most valid difference is that found in the comparison of the number of brothers and cousins who obtained a position in the starred group. From four times as many male cousins as brothers came fewer starred men.

I have computed similar ratios from the proportions reported by Galton[5] in his study of relatives of living fellows of the Royal Society whose names appeared in the year book of the society in 1904. Only male relatives are represented, and are as follows:

TABLE IX

| | Number | Number of Relatives Reduced to Comparable Ratios | Expressed in Per Cent. |
|---|---|---|---|
| Brothers | 104 | 104 | 40.3 |
| Fathers | 81 | 81 | 31.4 |
| Uncles | 97 | 48.5 | 18.8 |
| Cousins | 99 | 24.75 | 9.5 |
| Total | 381 | 258.25 | 100.0 |

In any judgment of the validity of the differences given above it is well to keep in mind the fact that the near relatives are more likely to be recorded and reported than the more remote. One might say that completeness of data is correlated directly with closeness of relationship, owing to the less exact knowledge concerning the more remotely related. Omissions are more likely to occur in the cousin relationships than in the brothers and more likely in the uncle relationship than in the fathers.

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[5] Noteworthy Families, p. xl.

Something of a check on results already given may be had by comparing the distribution of nephews and nieces with sons and daughters. Both groups should be comparable so far as age and numbers are concerned. Furthermore, all handbooks may be used since all persons concerned have had equal opportunity to achieve a place in the various lists. None is included in Appleton's "Cyclopedia."

TABLE X

| Relationship | Number of Those Distinguished | Reduced to Comparable Ratios | Reduced to Per Cent. |
|---|---|---|---|
| Sons and daughters........ | 18 | 18 | 75 |
| Nieces and nephews........ | 12 | 6 | 25 |
| Total................. | 30 | 24 | 100 |

The small number in each of the two groups does not permit any great confidence in reliability of the ratios, but the results are in agreement with the previous table. Table IV shows that five of the sons are found only in "American Men of Science." It might, therefore, be argued that a contributing factor causing the larger number of sons to be distinguished is the direction of the work. Sons, at least English sons, are said to be more likely than not to follow the occupation of the father. Since "American Men of Science" is restricted to scientific people and is a less fine selection than "Who's Who in America," the sons of scientific men are more likely to be included than sons and daughters of the uncles and aunts. If we eliminate those found only in "American Men of Science," we have the following:

TABLE XI

| | Number Distinguished | Reduced to Comparable Ratios | Reduced to Per Cent. |
|---|---|---|---|
| Sons and daughters........ | 13 | 13 | 70.3 |
| Nieces and nephews........ | 11 | 5.5 | 29.7 |
| Total................. | 25 | 18.5 | 100.0 |

It will be seen that the per cent. ratios remain substantially the same.

It is likely that the sons and daughters who are distinguished are more completely recorded than the nieces and nephews. The fact remains that these data are in agreement with those of all like studies. The nearer the kinship the greater the resemblance in distinction, and if distinction means special performance, the greater the resemblance in performance.

## RELATIONSHIPS MORE REMOTE THAN FIRST COUSIN

Numerous relatives of more remote degree than first cousin were reported and others were discovered by the writer. There were 60 first cousins of the parents of the men of science. Of these, 31 are cousins of the father and 29 cousins of the mother. The numbers are consistent with the other data, but the possibilities of error and incompleteness make the account of these and other remote relatives unusable at present except in the study of specialization of inheritance. The tedious and exacting work of deciphering relationships in remote degrees make the usefulness of doing so questionable in the present case.

There are 53 great uncles and great aunts, that is, uncles and aunts of the parents of the scientific men. This, again, is in agreement with the rest of the data. There are 21 great-grandparents. There are 82 relatives of a degree more remote than any mentioned and 43 of remote relationship, but of a degree not yet determined. A simple summary of these extra-statistical relatives is as follows:

TABLE XII

| | |
|---|---|
| First cousins of parents: | |
| (1) Cousins of father | 31 |
| (2) Cousins of mother | 29 |
| Great-uncles and aunts: | |
| (1) Uncles of father | 28 |
| (2) Uncles of mother | 25 |
| Great-grandparents: | |
| (1) Grandparents of father | 8 |
| (2) Grandparents of mother | 13 |
| More remote than any listed above | 82 |
| Total | 217 |
| Relationship unknown but known to be at least as remote as cousin of parent | 43 |
| Total | 260 |

## THE NUMBER OF PATERNAL AND MATERNAL RELATIVES OF DISTINCTION

Table XIII gives the distribution of relatives of distinction in two groups, the paternal and the maternal. The equality of the two groups is obvious. The differences in specific relationships, such as grandparents and cousins, may be of significance, but none is known. The difference in favor of the MF is, in fact, striking, but if explained as indicative of some advantageous maternal inheritance, some explanation for the size of the FBS group must be found.

TABLE XIII

| Relatives on Paternal Side Fathers Omitted | | Relatives on Maternal Side Mothers Omitted | |
|---|---|---|---|
| FB | 33 | MB | 31 |
| FSi | 4 | MSi | |
| FF | 17 | MF | 35 |
| FM | 1 | MM | 1 |
| FBS | 45 | MBS | 20 |
| FBD | | MBD | 1 |
| FSiS | 15 | MSiS | 18 |
| FSiD | 2 | MsiD | 4 |
| Total | 117 | Total | 110 |

MORE REMOTE RELATIVES

| | | | |
|---|---|---|---|
| Cousins of father | 31 | Cousins of mother | 29 |
| Uncles of father | 28 | Uncles of mother | 25 |
| Grandparents of father | 8 | Grandparents of mother | 13 |
| Total | 67 | Total | 67 |

The perfect agreement in the totals of the more remote relatives is indicative of a high degree of validity in the data, as are the totals in the near relatives account. The evidence for the truth of this statement is found in Galton's studies. His early studies, in which remote relationships were used, showed paternal relatives predominating over maternal at a ratio of seven to three. This ratio held closely for five of the eight groups of distinguished men. In two of the other three the differences were greater, being 95 to 6 for 16 relatives of great poets and 85 to 15 for 20 relatives of artists. The divines, however, showed an opposite ratio of 27 to 73.

Galton seemed to take these differences rather seriously and offered some curious explanations, such as possible lack of feminine attraction in women of families of high intellectual merit. But in his later work on "English Men of Science," he says:

> As regards the relative influence of paternal and maternal lines I find close equality. My method of comparison is by setting off paternal grandfathers and maternal uncles, no other degree of kinship being available for the purpose. My results for 100 scientific men are paternal grandfathers, public characters, 10, of high private reputation 3, paternal uncles 13 and 8, making a total on the paternal side of 34. On the other hand, the maternal grandfathers are 11 and 4, maternal uncles, 15 and 7, making a total on the maternal side of 37. . . . In Hereditary Genius, p. 196 having fewer cases to deal with I extended my inquiries to nephews and grandsons, and in a second table to great-grandparents, grandsons and other equally remote degrees, but this latter was confessedly of little value.[6]

The similarity in paternal and maternal groups holds in the case of science. There is a difference in favor of the maternal group, but it is thought that this difference is within limits determined by chance factors. The total number in the paternal group is 117, of whom 30.8 per cent. are classed as people of distinction in the field of science. The total number in the maternal group is 110, of whom 36.3 per cent. are classed as people of distinction in the field of science.

From a common-sense point of view these similarities are certainly unexpected. One would think that the di-

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[6] English Men of Science, 1874, p. 72.

TABLE XIV

MATERNAL AND PATERNAL RELATIVES DISTINGUISHED IN SCIENCE AND IN FIELDS OTHER THAN SCIENCE

| Paternal | | | Maternal | | |
|---|---|---|---|---|---|
| | Science | Non-science | | Science | Non-science |
| FF | 3 | 14 | MF | 10 | 25 |
| FM | | 1 | MM | | 1 |
| FB | 7 | 26 | MB | 9 | 22 |
| FSi | | 4 | MSi | | |
| FBS | 21 | 24 | MBS | 10 | 10 |
| FBD | | | MBD | 1 | |
| FSiS | 5 | 10 | MSiS | 9 | 9 |
| FSiD | | 2 | MSiD | 1 | 3 |
| | 36 | 81 | | 40 | 70 |
| Totals | 117 | | | 110 | |
| Differences in per cent | 30.8 | 69.2 | | 36.3 | 63.7 |

rection of a man's work is more likely to be directed by paternal social inheritance than maternal. The son has direct contact with the occupational activity of the father; his contact with the occupations of those on the maternal side are indirect in the sense that the mother is not likely to be engaged in a specific field other than domestic duties. Explanation can be made from the sociological or biological points of view; the fact remains that whatever environmental factors are causes of the direction and extent of achievement, there is no evidence of differential influence in paternal and maternal directions.

It is not unreasonable to expect that future ratings of youthful individuals for whom psychologists will predict a future will take account of the performance of their relatives. It is being proposed that more just methods of insurance would be in force if differential ratios were allowed on the basis of the length of life of the parents and grandparents of the person desiring insurance. Biologists and actuaries propose to predict length of life by "performance" of near relatives. It may be possible to equate the values of the different degrees of relationship as an item in the prediction of achievement.

The method used in this study has serious limitations, but in the present state of ignorance and difficulty of making measurements of the performance in question it gives results that are believed to be a distinct contribution to the fund of information on family resemblances. It may be that adequate measures of high intellectual performance will soon be discovered and perfected, but an enormous amount of measuring must be done before ideally scientific methods can give the data equivalent to that contained in this study. The long period concerned in the history of one generation, the difficulty of making objective measurements on closely related, and much more on the remotely related, together with the expense and persistence required, justifies the present method in spite of the limitations. We are referring now to intellectual performance of such an order that the life history of the individual becomes of public interest.

## SUMMARY

The data show (1) that a brother of a man of science is twice as likely to be distinguished as a father, four times as likely as an uncle and about six times as likely as a first cousin, and offspring three times as likely as nieces and nephews; (2) that paternal and maternal influences are not unequal; (3) that the number of relatives in the remote degrees though not strictly comparable show results consistent with the more complete accounts of those in the nearer.

(*To be continued*)

# EXPERIMENTAL STUDIES ON THE DURATION OF LIFE

## VII. The Mendelian Inheritance of Duration of Life in Crosses of Wild Type and Quintuple Stocks of Drosophila Melanogaster[1]

PROFESSOR RAYMOND PEARL, SYLVIA L. PARKER
AND B. M. GONZALEZ

### Introduction

There is now abundant evidence from at least two widely different organisms, *Drosophila* and man, that if duration of life be measured accurately for a considerable number of individuals, and these measurements be then treated as attributes or characters of the individuals which gave rise to them, the results over a series of generations are in fact precisely as they would be expected to be if duration of life were an inherited character, like stature or eye color (*cf.* Pearl, R. (52), for a review of the literature on which this statement is based). In the case of man the evidence is in the main statistical in character (but see Pearl, R. (53)) and gives directly no inkling as to the mechanism of the inheritance. In *Drosophila* Hyde (11) showed that the character appeared to be inherited in a Mendelian manner, and Pearl and Parker (32) have demonstrated the constancy of definite degrees of mean longevity in inbred strains or lines of the same organism. There is needed, however, much more intensive investigation of the exact mode and mechanism of inheritance of this character in *Drosophila,* in spite of the excellent pioneer work of Hyde, which we have been able to confirm in every essential particular. This and the next following paper in this series will be devoted to the discussion of results which have so far been obtained in this field in the work of this laboratory. The present paper will give the analysis of data resulting from extensive experiments in crossing wild type flies of our Old Falmouth stock (*cf.* Pearl and Parker (27, p. 486)) with the short-lived Quintuple stock.

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[1] Papers from the Department of Biometry and Vital Statistics, School of Hygiene and Public Health, Johns Hopkins University. No. 84.

Complete life tables for wild type flies, of which the Old Falmouth stock is representative, and for Quintuple flies, have been presented in the first of these Studies. The wide difference in the two stocks crossed in the present experiments is sufficiently indicated by the fact that for wild type males the expectation of life ($e_0$) at emergence is 41.0 days and for Quintuple males is only 14.2 days. For females the corresponding $e_0$ figures are 38.8 and 15.8 days, respectively. We are thus dealing with well-defined, indeed widely different, grades or degrees of the character in the two stocks in these experiments.

## MATERIAL AND METHODS

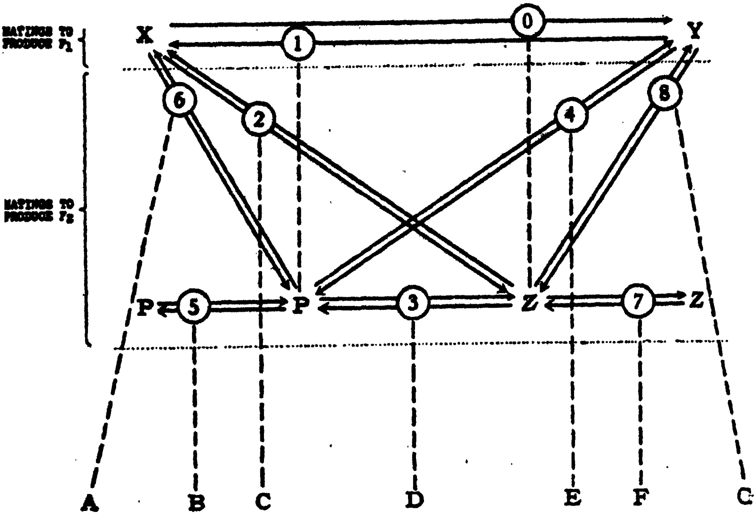
The data on duration of life of the parental stocks used in these experiments were obtained from the progeny of 4 individual (brother and sister) matings in each of the two stocks Old Falmouth and Quintuple, made on April 7–9, 1920. The offspring flies emerged between April 17 and May 5, 1920. The original parents were transferred to new mating bottles 8 days after the first bottle, in each case, was started.

The $F_1$ flies were derived from one mass mating of each of the possible reciprocal crosses. These matings were of 6 pairs of flies each, taken at random from the stock bottles of the two sorts used. The matings were made April 20, 1920, and the flies emerged April 30–May 14. The parents were transferred to new breeding bottles 8 days after the first bottles were started.

The matings to produce $F_2$ and $F_3$ generations are designated throughout this paper on the standard plan described some years ago by Pearl (54). In order to save reference to that paper Table I is reproduced from it here. In the present case X = Quintuple, and Y = Old Falmouth.

## TABLE I

MATINGS TO PRODUCE $F_3$



| $F_2$ Individuals Mated | Number of Mating | $F_2$ Individuals Mated | Number of Mating | $F_2$ Individuals Mated | Number of Mating | $F_2$ Individuals Mated | Number of Mating |
|---|---|---|---|---|---|---|---|
| *A* × *X* | 10 | *B* × *Z* | 46 | *C* × *F* | 51 | *E* × *E* | 19 |
| *A* × *Y* | 12 | *B* × *B* | 13 | *C* × *G* | 53 | *E* × *F* | 45 |
| *A* × *P* | 40 | *B* × *C* | 37 | *D* × *X* | 22 | *E* × *G* | 47 |
| *A* × *Z* | 42 | *B* × *D* | 29 | *D* × *Y* | 24 | *F* × *X* | 30 |
| *A* × *A* | 11 | *B* × *E* | 55 | *D* × *P* | 52 | *F* × *Y* | 32 |
| *A* × *B* | 33 | *B* × *F* | 57 | *D* × *Z* | 54 | *F* × *P* | 60 |
| *A* × *C* | 25 | *B* × *G* | 59 | *D* × *D* | 17 | *F* × *Z* | 62 |
| *A* × *D* | 35 | *C* × *X* | 18 | *D* × *E* | 43 | *F* × *F* | 21 |
| *A* × *E* | 61 | *C* × *Y* | 20 | *D* × *F* | 31 | *F* × *G* | 49 |
| *A* × *F* | 63 | *C* × *P* | 48 | *D* × *G* | 27 | *G* × *X* | 34 |
| *A* × *G* | 65 | *C* × *Z* | 50 | *E* × *X* | 26 | *G* × *Y* | 36 |
| *B* × *X* | 14 | *C* × *C* | 15 | *E* × *Y* | 28 | *G* × *P* | 64 |
| *B* × *Y* | 16 | *C* × *D* | 39 | *E* × *P* | 56 | *G* × *Z* | 66 |
| *B* × *P* | 44 | *C* × *E* | 41 | *E* × *Z* | 58 | *G* × *G* | 23 |

Table II gives the data regarding the matings to produce the $F_2$ and $F_3$ generations.

In all the experiments recorded in this paper the only one of the five somatic mutant characters carried in the Quintuple stock to which any attention was paid was *vestigial wing*. Individuals were not recorded at all in

T II

DATA ON MATINGS TO PRODUCE $F_2$ AND $F_3$

| General Type of Mating | Type of Progeny Flies | Type of Mating | Mating No. | Date of Mating (all 1920) | Type of Parents | | No. Parents Mated | | Date of Emergence of Parents | | Date of Emergence of Progeny | No. of Progeny | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | | Wild Type | Vestigial |
| $F_1 \times F_1$ ............... | F | (7) | 72 | 5/1 | Z | Z | 4 | 4 | 5/1 | 5/1 | 5/10–18 | 115 | 19 |
| $F_1 \times F_1$ ............... | B | (5) | 73 | 5/1 | P | P | 4 | 4 | 5/1 | 5/1 | 5/10–18 | 56 | 7 |
| $F_1 \times F_1$ ............... | F | (7) | 74 | 5/4 | Z | Z | 6 | 6 | 5/4 | 5/4 | 5/13–21 | 109 | 22 |
| $F_1 \times F_1$ ............... | B | (5) | 75 | 5/4 | P | P | 6 | 6 | 5/4 | 5/4 | 5/13–21 | 146 | 56 |
| $F_1 \times F_1$ ............... | D | (3) | 76 | 5/20 | P | Z | 2 | 2 | 5/8 | 5/8 | 5/29–6/6 | 115 | 10 |
| $F_1 \times F_1$ ............... | D | (3) | 77 | 5/20 | Z | P | 2 | 2 | 5/7 | 5/8 | 5/29–6/6 | 98 | 34 |
| | | | | | | | | | | | | 639 | 148 |
| $F_1$ × Quintuple.......... | C | (2) | 78 | 5/20 | Quin. | Z | 1 | 1 | 5/20 | 5/13 | 5/28–6/4 | 64 | 72 |
| $F_1$ × Quintuple.......... | C | (2) | 79 | 5/20 | Z | Quin. | 4 | 4 | 5/7 | 5/20 | 5/30–6/6 | 24 | 44 |
| $F_1$ × Quintuple.......... | A | (6) | 82 | 5/20 | Quin. | P | 1 | 1 | 5/20 | 5/8 | 5/29–6/6 | 75 | 70 |
| $F_1$ × Quintuple.......... | A | (6) | 83 | 5/20 | P | Quin. | 4 | 4 | 5/8 | 5/20 | 5/29–6/6 | 54 | 80 |
| | | | | | | | | | | | | 217 | 266 |
| $F_1$ × Old Fal............ | G | (8) | 80 | 5/20 | O.F. | Z | 1 | 1 | 5/20 | 5/13 | 5/28–6/5 | 142 | — |
| $F_1$ × Old Fal............ | G | (8) | 81 | 5/20 | Z | O.F. | 4 | 4 | 5/7 | 5/20 | 5/30–6/6 | 175 | — |
| $F_1$ × Old Fal............ | E | (4) | 84 | 5/20 | O.F. | P | 1 | 1 | 5/20 | 5/8 | 5/28–6/5 | 163 | — |
| $F_1$ × Old Fal............ | E | (4) | 85 | 5/20 | P | O.F. | 4 | 6 | 5/8 | 5/20 | 5/29–6/6 | 202 | — |
| | | | | | | | | | | | | 682 | — |
| $F_1$ ♂ × $F_2$ Vest. ♀ ...... | — | 54 | 86 | 6/1 | Z | $D_{76}$ | 3 | 3 | 5/9 | 5/29 | 6/9–17 | 76 | 121 |
| $F_1$ ♂ × $F_2$ Vest. ♀ ...... | — | 52 | 88 | 6/1 | P | $D_{76}$ | 3 | 3 | 5/10 | 5/30 | 6/10–18 | 95 | 107 |
| $F_1$ ♂ × $F_2$ Vest. ♀ ...... | — | 54 | 90 | 6/1 | Z | $D_{77}$ | 3 | 3 | 5/9 | 5/29 | 6/9 –17 | 67 | 76 |
| $F_1$ ♂ × $F_2$ Vest. ♀ ...... | — | 52 | 92 | 6/1 | P | $D_{77}$ | 3 | 3 | 5/10 | 5/29 | 6/9 –17 | 63 | 119 |
| | | | | | | | | | | | | 301 | 423 |
| $F_1$ ♂ × $F_2$ Wild ♀ ...... | — | 54 | 87 | 6/1 | Z | $D_{76}$ | 3 | 3 | 5/9 | 6/1 | 6/10–18 | 155 | 55 |
| $F_1$ ♂ × $F_2$ Wild ♀ ...... | — | 52 | 89 | 6/1 | P | $D_{76}$ | 3 | 3 | 5/9 | 5/30 | 6/9 –17 | 175 | 0 |
| $F_1$ ♂ × $F_2$ Wild ♀ ...... | — | 54 | 91 | 6/1 | Z | $D_{77}$ | 3 | 3 | 5/9 | 5/28 | 6/10–18 | 163 | 2 |
| $F_1$ ♂ × $F_2$ Wild ♀ ...... | — | 52 | 93 | 6/1 | P | $D_{77}$ | 3 | 3 | 5/9 | 5/28 | 6/9 –17 | 152 | 7 |
| | | | | | | | | | | | | 645 | 64 |

respect of the other four, purple, speck, arc and black. This was deliberate. We desired to deal only with that one of the five mutations which earlier experiments had shown to be definitely and markedly related to duration of life, and which at the same time easily identified the flies morphologically. In the next paper in this series each of the 5 mutations in Quintuple will be dealt with separately in relation to duration of life. The experiments here recorded were all carried out in accordance with the standard procedure described in the earlier papers in this series. All determinations of duration of life were made in incubators at 25° C. The food and other environmental conditions were as constant and identical for all groups as it was possible to make them. In tabulating and analyzing the results both sexes are treated together.

TABLE III

Death and Survivorship Distributions for P and $F_1$ Generations

| Age in Days | Old Falmouth | | Old Falmouth ♂ × Quintuple ♀ (Mating Type (1)) | | Quintuple ♂ × Old Falmouth ♀ (Mating Type (0)) | | All $F_1$'s | | Age in Days | Quintuple | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | $d_x'$ | $l_x'$ | $d_x'$ | $l_x'$ | $d_x'$ | $l_x'$ | $d_x'$ | $l_x'$ | | $d_x'$ | $l_x'$ |
| 1– 5 | 19 | 1,000 | 1 | 1,000 | 2 | 1,000 | 3 | 1,000 | 1– 2 | 19 | 1,000 |
| 6–11 | 14 | 970 | 0 | 993 | 6 | 994 | 6 | 993 | 3– 5 | 27 | 953 |
| 12–17 | 21 | 948 | 2 | 993 | 5 | 977 | 7 | 982 | 6– 8 | 47 | 886 |
| 18–23 | 27 | 915 | 7 | 980 | 4 | 962 | 11 | 968 | 9–11 | 71 | 769 |
| 24–29 | 38 | 872 | 12 | 934 | 22 | 951 | 34 | 946 | 12–14 | 72 | 592 |
| 30–35 | 63 | 812 | 6 | 854 | 16 | 887 | 22 | 877 | 15–17 | 66 | 413 |
| 36–41 | 65 | 712 | 12 | 815 | 16 | 841 | 28 | 833 | 18–20 | 43 | 249 |
| 42–47 | 90 | 609 | 9 | 735 | 61 | 795 | 70 | 777 | 21–23 | 18 | 142 |
| 48–53 | 84 | 467 | 18 | 675 | 43 | 618 | 61 | 636 | 24–26 | 19 | 97 |
| 54–59 | 107 | 334 | 37 | 556 | 61 | 494 | 98 | 513 | 27–29 | 10 | 50 |
| 60–65 | 72 | 165 | 27 | 311 | 42 | 318 | 69 | 316 | 30–32 | 6 | 25 |
| 66–71 | 23 | 51 | 14 | 132 | 41 | 197 | 55 | 177 | 33–35 | 3 | 10 |
| 72–77 | 7 | 14 | 6 | 40 | 24 | 78 | 30 | 66 | 36–38 | 1 | 2 |
| 78–83 | 0 | 3 | — | 0 | 3 | 9 | 3 | 6 | 39–41 | — | 0 |
| 84–89 | 2 | 3 | — | — | — | 0 | — | 0 | — | — | — |
| 90–95 | — | 0 | — | — | — | — | — | — | — | — | — |
| Totals | 632 | — | 151 | — | 346 | — | 497 | — | — | 402 | — |

## PARENTAL AND $F_1$ GENERATIONS

The observed death distributions and the survivorship distributions calculated therefrom, for (a) the two parental stocks, (b) the $F_1$ individuals from reciprocal crosses, and (c) the combined $F_1$'s are given in Table III. In this and all similar tables throughout the paper, the figures entered in the $d_x'$ columns are the observed number of flies dying *within* the age interval indicated in the age column, and the figures in the $l_x'$ column are the numbers of survivors out of 1,000 starting imaginal life together, *at the beginning of each age interval.*

The survivorship distributions of Table III are shown graphically, on an arithlog grid, in Fig. 1.

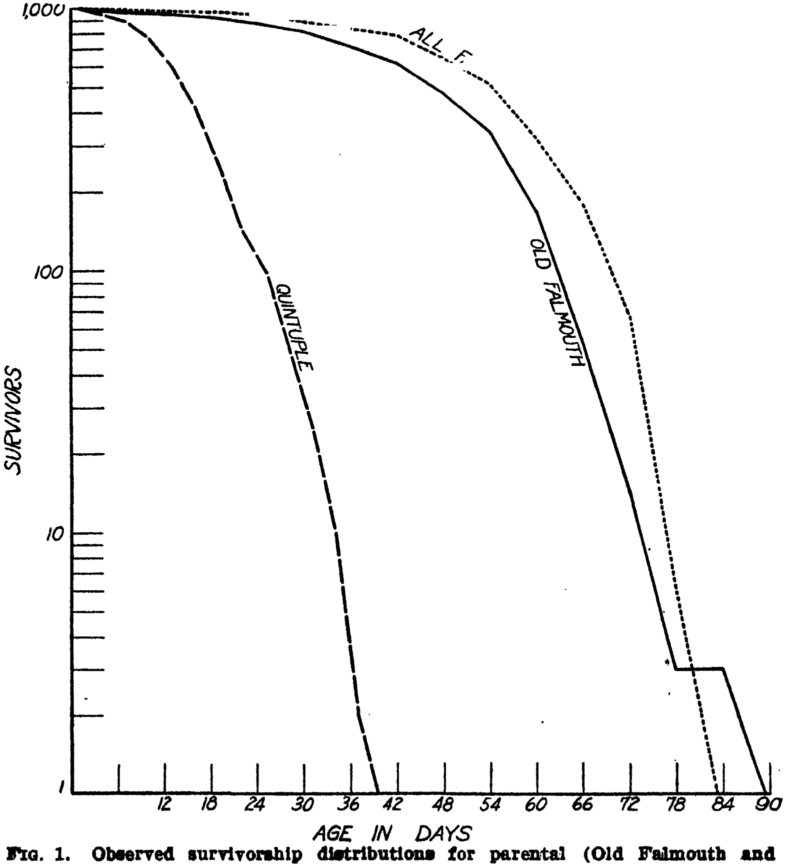


FIG. 1. Observed survivorship distributions for parental (Old Falmouth and Quintuple) and $F_1$.

The biometric constants calculated from the $d_x'$ distributions of Table III are presented in Table IV.

TABLE IV

Biometric Constants for Duration of Life of Parental and $F_1$ Flies

| Group | Mating Type | Mean Age at Death | Standard Deviation | Coefficient of Variation |
|---|---|---|---|---|
| Parental Old Falmouth..... | — | 44.26±.44 days | 16.57±.31 | 37.44± .80 |
| Quintuple........ | — | 14.08±.23 days | 6.93±.16 | 49.23±1.43 |
| Quint. ♂ × Old Fal. ♀ | (0) | 51.73±.57 days | 15.71±.40 | 30.37± .85 |
| $F_1$ Old Fal. ♂ × Quint. ♀ | (1) | 51.12±.84 days | 15.29±.59 | 29.90±1.26 |
| All $F_1$'s .............. | (0)+(1) | 51.55±.47 days | 15.58±.33 | 30.23± .70 |

From the data so far presented we note the following points:

1. In these experiments we are crossing two strains of *Drosophila* of widely different average duration of life and forms of life curve. The wild type Old Falmouth parent stock has a mean duration of life more than three times as great as that of the Quintuple parent stock. This difference is so great, and the two stocks are so constant in the maintenance of their characteristic mean longevities, that there can be no question that we are crossing two distinct biological entities perfectly discontinuous in respect of the character dealt with. The two stocks differ fundamentally not only in respect of mean duration of life but also in respect of variation in the time of dying.

2. The $F_1$ generation progeny from the cross are structurally like the wild type parent. That is to say, the $F_1$ flies are to a first degree of approximation indistinguishable in their morphology from the wild type parent. The morphological mutations carried by the Quintuple flies behave as Mendelian recessives to their wild type allelomorphs. Also the duration of life in the $F_1$ flies is essentially similar to that established by their wild type (Old Falmouth) parent. They are long-lived flies. In actual fact the $F_1$'s have a somewhat longer mean duration of life than the long-lived, wild type par-

ent. Taking all $F_1$'s together the difference in the mean is $51.55 - 44.26 = 7.29 \pm .64$ days. This is a certainly significant difference amounting to 11.4 times its probable error. The $l_x'$ lines in Fig. 1 show plainly the superior longevity of the $F_1$'s over the longer lived parent. This phenomenon is objectively similar to the enhanced vigor observed in the first generation plants in crosses of maize, as described by East and Jones (55), Shull (56) and others. It probably has the same explanation.

3. There is no significant difference in respect of duration of life between the reciprocal crosses. The mean duration of life and the variability is identical whether the cross-bred individuals had a wild type father or mother. This is to be expected for the structural characters of the fly, at least, because none of the mutations in the Quintuple stock exhibits sex-linked inheritance, and they have therefore had their genes assigned to another (the second) than the X chromosome. Duration of life in this respect behaves in inheritance exactly like the morphological mutations with which it is associated in this cross.

4. The $F_1$ flies are significantly less variable relatively in duration of life than are either of the parent stocks. In view of the close parallelism between inheritance of morphological characters and inheritance of duration of life which has so far been noted (and which will be shown as we proceed to extend to many other genetic relationships), what one would like to know is whether the $F_1$'s are less variable in structural characteristics than are the parent forms. We have no data on this point for the flies with which we have worked.

## $F_2$ GENERATIONS

Since use was made of wing form (normal wild type versus vestigial wing) to distinguish the flies morphologically in this generation, attention is directed first to the Mendelian segregation of this structural character. Table V gives the data. In this table each mating is

## TABLE V

### Mendelian Segregation in $F_2$ of Normal and Vestigial Wing, Tabulated by Separate Matings

| Mating Type | Numbers of $F_2$ Flies with Wings | | | Probable Errors | Deviation / P. E. Dev. | Probable Times of Occurrence of Such a Deviation in 100 Trials | Mating No. |
|---|---|---|---|---|---|---|---|
| | Normal | Vestigial | Total | | | | |
| (5) P × P | 56 | 7 | 63 | | | | 73 |
| *Expected* | *47.25* | *15.75* | *63* | ±2.32 | 3.8 | 1.04 | |
| (5) P × P | 146 | 56 | 202 | | | | 75 |
| *Expected* | *151.5* | *50.5* | *202* | ±4.15 | 1.3 | 38.06 | |
| (5) Total | 202 | 63 | 265 | | | | 73+75 |
| *Expected* | *198.75* | *66.25* | *265* | ±4.76 | .7 | 50 | |
| (3) P ♂ × Z ♀ | 115 | 10 | 125 | | | | 76 |
| *Expected* | *93.75* | *31.25* | *125* | ±3.27 | 6.5 | .005 | |
| (3) Z ♂ × P ♀ | 98 | 34 | 132 | | | | 77 |
| *Expected* | *99* | *33* | *132* | ±3.36 | .3 | 50 | |
| (3) Total | 213 | 44 | 257 | | | | 76+77 |
| *Expected* | *192.75* | *64.25* | *257* | ±4.68 | 4.3 | .37 | |
| (7) Z × Z | 115 | 19 | 134 | | | | 72 |
| *Expected* | *100.5* | *33.5* | *134* | ±3.38 | 4.3 | .37 | |
| (7) Z × Z | 109 | 22 | 131 | | | | 74 |
| *Expected* | *98.25* | *32.75* | *131* | ±3.34 | 3.2 | 3.09 | |
| (7) Total | 224 | 41 | 265 | | | | 72+74 |
| *Expected* | *198.75* | *66.25* | *265* | ±4.75 | 5.3 | .05 | |
| All *inter se* $F_1$ matings (3, 5 and 7) | 639 | 148 | 787 | | | | 73+75+76 +77+72+74 |
| *Expected* | *590.25* | *196.75* | *787* | ±9.46 | 5.0 | .074 | |
| (2) Vest. ♂ × Z ♀ | 64 | 72 | 136 | | | | 78 |
| *Expected* | *68* | *68* | *136* | ±3.93 | 1.0 | 50 | |
| (2) Z ♂ × Vest. ♀ | 24 | 44 | 68 | | | | 79 |
| *Expected* | *34* | *34* | *68* | ±2.78 | 3.6 | 1.52 | |
| (2) Total | 88 | 116 | 204 | | | | 78+79 |
| *Expected* | *102* | *102* | *204* | ±4.82 | 2.9 | 5.05 | |
| (6) Vest. ♂ × P ♀ | 75 | 70 | 145 | | | | 82 |
| *Expected* | *72.5* | *72.5* | *145* | ±4.06 | .6 | 50 | |

TABLE V (*Continued*)

| Mating Type | Numbers of $F_2$ Flies with Wings | | | Probable Errors | Deviation / P. E. Dev. | Probable Times of Occurrence of Such a Deviation in 100 Trials | Mating No. |
|---|---|---|---|---|---|---|---|
| | Normal | Vestigial | Total | | | | |
| (6) P ♂ × Vest. ♀ | 54 | 80 | 134 | | | | 83 |
| *Expected* | *67* | *67* | *134* | ±3.38 | 3.8 | 1.04 | |
| (6) Total | 129 | 150 | 279 | | | | 82+83 |
| *Expected* | *139.5* | *139.5* | *279* | ±5.63 | 1.9 | 20.00 | |
| (2) All back and crosses of<br>and<br>(6) $F_1$ on Vestig. | 217 | 252 | 469 | | | | 78+79+82+83 |
| *Expected* | *234.5* | *234.5* | *469* | ±7.30 | 2.4 | 10.55 | |
| (8) Wild ♂ × Z ♀ | 142 | 0 | 142 | | | | 80 |
| *Expected* | *142* | *0* | *142* | — | — | — | |
| (8) Z ♂ × wild ♀ | 175 | 0 | 175 | | | | 81 |
| *Expected* | *175* | *0* | *175* | — | — | — | |
| (2) Wild ♂ × P ♀ | 163 | 0 | 163 | | | | 84 |
| *Expected* | *163* | *0* | *163* | — | — | — | |
| (2) P ♂ × wild ♀ | 202 | 0 | 202 | | | | 85 |
| *Expected* | *202* | *0* | *202* | — | — | — | |

given separately. The probable errors of the Mendelian ratios are on the basis of $\sqrt{npq}$ as the standard deviation of the class. The actual values of the probable errors are taken from the extremely useful set of "Tables of Probable Errors of Mendelian Ratios" issued by the Department of Plant Breeding of Cornell University.

In general the observed results in respect of the inheritance of vestigial wings appear at first glance to be not in especially bad accord with Mendelian expectation. There are, however, certain systematic divergences which should be noted. These are:

1. The $F_1$ *inter se* matings (P × P, P × Z and Z × Z), when taken as a whole, give a highly improbable, indeed certainly significant, divergence from the expected 3 : 1 ratio. Only 7 times in 10,000 trials with samples of 787 individuals should we expect in random sampling to get so great a deviation of fact from theory as that actually shown. The divergence is in the direction of *too few* vestigials. This divergence is due more to P × Z than to either of the other two mating types, P × P giving indeed a significantly non-divergent result.

2. The $F_1$ back crosses upon vestigial give a more probable, but still by no means satisfactory, agreement with theory. Only about once in 10 trials would as great (or greater) deviation as that realized be expected in random sampling. But the divergence is in the direction of *too many* vestigials.

3. The relations stated in 1 and 2 above mean that whenever the genes for vestigial were contributed to $F_2$ zygotes from individuals duplex for this character (but in the back crosses) the progeny showed an excess of vestigial as compared with wild type flies, whereas when the vestigial genes came from individuals simplex in respect of this character (as in the $F_1$ *inter se* matings) there was a defect of vestigial flies in the progeny. What may be the ultimate meaning or explanation of this fact we shall not discuss now, but it seems advisable to point it out as a fact.

TABLE VI

DEATH AND SURVIVORSHIP DISTRIBUTION FOR WILD TYPE $F_2$ FLIES, DERIVED FROM *inter se* MATINGS OF $F_1$

| Age in Days | P × P (5) | P × P (5) | P × P (5) | | P ♂ × Z ♀ (3) | Z ♂ × P ♀ (3) | P × Z (3) | | Z × Z (7) | Z × Z (7) | Z × Z (7) | | All $F_1$ *Inter Se* Matings 72–77 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mating 73 | Mating 75 | Total | | Mating 76 | Mating 77 | Total | | Mating 72 | Mating 74 | Total | | | |
| | $d_x'$ | $d_x'$ | $d_x'$ | $l_x'$ | $d_x'$ | $d_x'$ | $d_x'$ | $l_x'$ | $d_x'$ | $d_x'$ | $d_x'$ | $l_x'$ | $d_x'$ | $l_x'$ |
| 1– 5 | — | 1 | 1 | 1,000 | 1 | 2 | 3 | 1,000 | 5 | 5 | 10 | 1,000 | 14 | 1,000 |
| 6–11 | — | 7 | 7 | 995 | — | 2 | 2 | 986 | — | 1 | 1 | 955 | 10 | 978 |
| 12–17 | — | 6 | 6 | 960 | 3 | 4 | 7 | 977 | 1 | 2 | 3 | 951 | 16 | 962 |
| 18–23 | 1 | 6 | 7 | 931 | 8 | 21 | 29 | 944 | 3 | 4 | 7 | 937 | 43 | 937 |
| 24–29 | 1 | 13 | 14 | 896 | 24 | 7 | 31 | 808 | 3 | 15 | 18 | 906 | 63 | 870 |
| 30–35 | 5 | 3 | 8 | 827 | 17 | 13 | 30 | 662 | 3 | 5 | 8 | 826 | 46 | 772 |
| 36–41 | 2 | 13 | 15 | 787 | 13 | 13 | 26 | 521 | 3 | 12 | 15 | 790 | 56 | 700 |
| 42–47 | 17 | 18 | 35 | 713 | 16 | 13 | 29 | 399 | 38 | 23 | 61 | 723 | 125 | 612 |
| 48–53 | 15 | 24 | 39 | 540 | 8 | 10 | 18 | 263 | 17 | 17 | 34 | 451 | 91 | 416 |
| 54–59 | 9 | 29 | 38 | 347 | 22 | 9 | 31 | 178 | 11 | 10 | 21 | 299 | 90 | 274 |
| 60–65 | 3 | 20 | 23 | 158 | 3 | 3 | 6 | 33 | 13 | 9 | 22 | 205 | 51 | 133 |
| 66–71 | — | 4 | 4 | 45 | 0 | 1 | 1 | 5 | 15 | 6 | 21 | 107 | 26 | 53 |
| 72–77 | 3 | 2 | 5 | 25 | — | 0 | 0 | 0 | 3 | 0 | 3 | 13 | 8 | 13 |
| 78–83 | 0 | 0 | 0 | 0 | — | — | — | — | 0 | — | 0 | 0 | 0 | 0 |
| Totals | 56 | 146 | 202 | — | 115 | 98 | 213 | — | 115 | 109 | 224 | — | 639 | — |

Turning now to the consideration of duration of life in the $F_2$ progeny we have in Tables VI and VII the data for wild type $F_2$ flies derived from *inter se* matings (P × P, P × Z, Z × Z) of $F_1$.

The $l_x'$ lines for the three total groups P × P, P × Z, and Z × Z and the original wild type parent are shown graphically in Fig. 2.

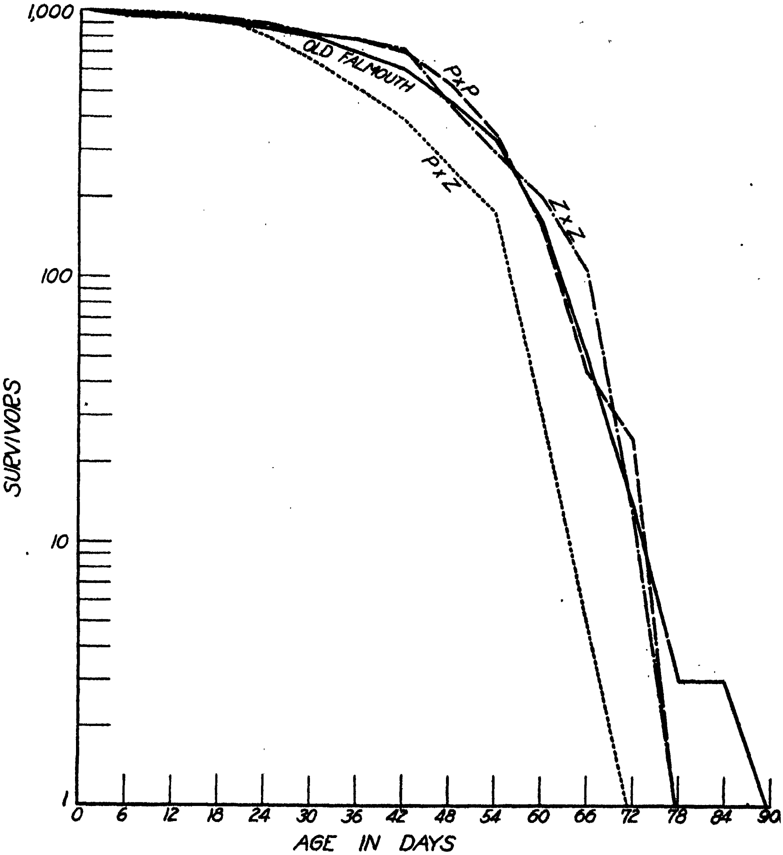


FIG. 2. Survivorship lines for $F_2$ wild type flies from $F_1$'s mated *inter se*. Dash line = P × P; dot line = P × Z; dash-dot line = Z × Z; solid line = original wild type parent stock.

From these data we note the following points regarding the wild type $F_2$'s from *inter se* matings of $F_1$:

1. Taking all such flies together, they have come back almost exactly in duration of life to the same mean and

variability, both absolute and relative, as the original Old Falmouth parental stock. The segregation in respect of long life in this cross appears therefore to be quantitatively perfect, and to have followed exactly the morphological segregation of wing form, the difference of the constants for the total distribution (last line of Table VII) being not significantly different (or indeed approaching significance) from those of the Old Falmouth parent (first line of Table IV).

TABLE VII

BIOMETRIC CONSTANTS FOR DURATION OF LIFE OF WILD TYPE $F_2$ FLIES FROM *inter se* MATINGS OF $F_1$

| Mating | Type | Mean Age at Death | Standard Deviation | Coefficient of Variation |
|---|---|---|---|---|
| P × P (Total) | (5) | 46.34 ± .73 days | 15.29 ± .51 days | 33.00 ± 1.22 |
| P ♂ × Z ♀ (76)... | (3) | 39.16 ± .83 days | 13.26 ± .59 days | 33.86 ± 1.67 |
| Z ♂ × P ♀ (77)... | (3) | 35.89 ± 1.01 days | 14.78 ± .71 days | 41.18 ± 2.30 |
| P × Z (Total) | (3) | 37.66 ± .65 days | 14.08 ± .46 days | 37.37 ± 1.38 |
| Z × Z (Total) | (7) | 46.01 ± .73 days | 16.19 ± .52 days | 35.19 ± 1.25 |
| All *inter se* matings. | (5) + (3) + (7) | 43.33 ± .42 days | 15.75 ± .30 days | 36.34 ± .77 |

2. The two similar *inter se* mating types, P × P and Z × Z, give substantially identical results for duration of life, neither means nor variability differing significantly.

3. The cross *inter se* mating type, P × Z, has a significantly lower mean duration of life than either of the other two types. The differences are:

$$\text{For } P \times P,\ 46.34 - 37.66 = 8.68 \pm .98 \text{ days}$$
$$\text{For } Z \times Z,\ 46.01 - 37.66 = 8.35 \pm .98 \text{ days}$$

In variability there is no certainly significant difference.

The corresponding data to Tables VI and VII, but for vestigial winged $F_2$'s are presented in Tables VIII and IX.

The $l_x'$ lines for the three total groups and the original vestigial parent stock are shown graphically in Fig. 3.

## TABLE VIII

DEATH AND SURVIVORSHIP DISTRIBUTION FOR VESTIGIAL F$_2$ FLIES, DERIVED FROM *inter se* MATINGS OF F$_1$

| Age in Days | P × P (5) | | | | P ♂ × Z ♀ (3) | Z ♂ × P ♀ (3) | P × Z (3) | | Z × Z (7) | | | | All F$_1$ *Inter Se* Matings | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mating 73 | Mating 75 | Total | | Mating 76 | Mating 77 | Total | | Mating 72 | Mating 74 | Total | | 72–77 | |
| | $d_x'$ | $d_x'$ | $d_x'$ | $l_x'$ | $d_x'$ | $d_x'$ | $d_x'$ | $l_x'$ | $d_x'$ | $d_x'$ | $d_x'$ | $l_x'$ | $d_x'$ | $l_x'$ |
| 1– 2 | 1 | 3 | 4 | 1,000 | 1 | 1 | 2 | 1,000 | 5 | 2 | 7 | 1,000 | 13 | 1,000 |
| 3– 5 | 2 | 18 | 20 | 937 | 2 | 2 | 4 | 955 | 12 | 3 | 15 | 829 | 39 | 912 |
| 6– 8 | — | 3 | 3 | 619 | — | 1 | 1 | 864 | 1 | — | 1 | 463 | 5 | 649 |
| 9–11 | — | 8 | 8 | 571 | 1 | 3 | 4 | 841 | 1 | 2 | 3 | 439 | 15 | 615 |
| 12–14 | 1 | 2 | 3 | 444 | — | 2 | 2 | 750 | — | 2 | 2 | 366 | 7 | 514 |
| 15–17 | 1 | 5 | 6 | 397 | — | 4 | 4 | 705 | — | 2 | 2 | 317 | 12 | 466 |
| 18–20 | — | 1 | 1 | 317 | — | 8 | 8 | 614 | — | — | — | 268 | 9 | 385 |
| 21–23 | — | 10 | 10 | 302 | 2 | 5 | 7 | 432 | — | 1 | 1 | 268 | 18 | 324 |
| 24–26 | — | 5 | 5 | 127 | 2 | 3 | 5 | 273 | — | 2 | 2 | 244 | 12 | 203 |
| 27–29 | — | 1 | 1 | 48 | 2 | 3 | 5 | 159 | — | 3 | 3 | 195 | 9 | 122 |
| 30–32 | — | — | — | 32 | — | 1 | 1 | 45 | — | 3 | 3 | 122 | 4 | 61 |
| 33–35 | 1 | — | 1 | 32 | — | 1 | 1 | 23 | — | — | — | 49 | 2 | 34 |
| 36–38 | — | — | — | 16 | — | — | — | 0 | — | — | — | 49 | — | 20 |
| 39–41 | 1 | — | 1 | 16 | — | — | — | — | — | — | — | 49 | 1 | 20 |
| 42–44 | — | — | — | 0 | — | — | — | — | — | — | — | 49 | — | 14 |
| 45–47 | — | — | — | — | — | — | — | — | — | 2 | 2 | 49 | 2 | 14 |
| 48–50 | — | — | — | — | — | — | — | — | — | — | — | 0 | — | 0 |
| Totals | 7 | 56 | 63 | — | 10 | 34 | 44 | — | 19 | 22 | 41 | — | 148 | — |

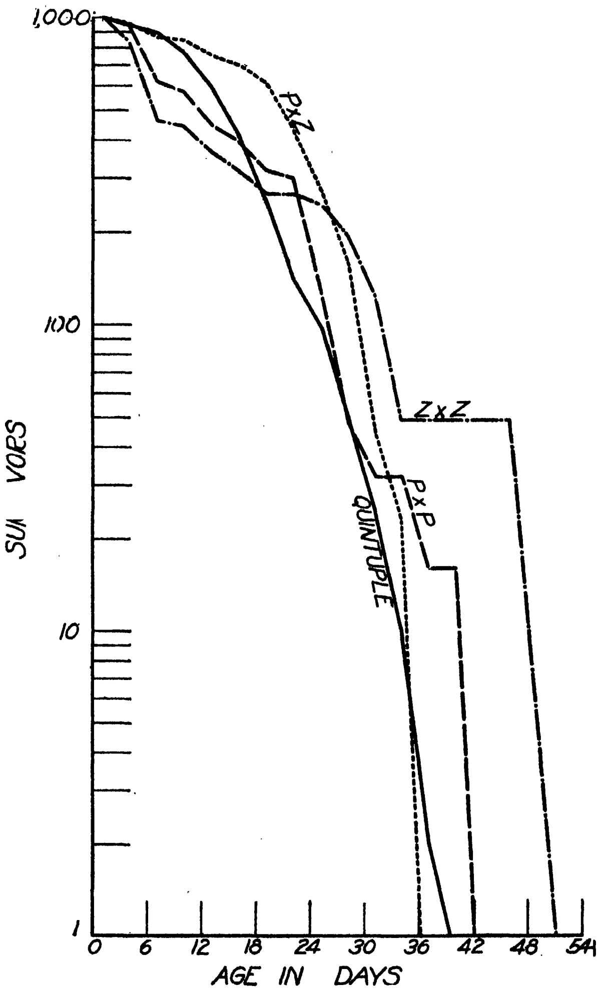


FIG. 3. Survivorship lines for $F_2$ vestigial flies from $F_1$'s mated *inter se*. Dash line = P x P; dot line = P x Z; dash-dot line = Z x Z; solid line = original vestigial parent stock.

From these data we note:

1. Taking all vestigial $F_2$ flies from *inter se* matings together, the distribution of mortality agrees in an extraordinarily close manner with that of the original vestigial parent stock (*cf.* Tables III and IV). The mean duration of life of the original vestigial parent stock was 14.08 ± .23 days and that of the $F_2$ vestigials from *inter se* matings is 14.60 ± .57 days. The segrega-

tion in respect of mean longevity is plainly exact and precise. The variability, both absolute and relative, is probably significantly higher in the $F_2$ than in the P flies (vestigials), but the $F_2$ samples are not large and too much stress is not to be laid upon these differences.

TABLE IX

BIOMETRIC CONSTANTS FOR DURATION OF LIFE OF VESTIGIAL $F_2$ FLIES FROM *inter se* MATINGS OF $F_1$

| Mating | Type | Mean Age at Death | Standard Deviation | Coefficient of Variation |
|---|---|---|---|---|
| P × P (Total) | (5) | 13.10 ± .79 days | 9.26 ± .54 days | 70.70 ± 6.01 |
| P ♂ × Z ♀ (76)... | (3) | 17.45 ± 2.18 days | 10.23 ± 1.54 days | 58.64 ± 11.49 |
| Z ♂ × P ♀ (77)... | (3) | 18.81 ± .89 days | 7.67 ± .63 days | 40.78 ± 3.85 |
| P × Z (Total) | (3) | 18.50 ± .85 days | 8.34 ± .60 days | 45.09 ± 3.85 |
| Z × Z (Total) | (7) | 13.15 ± 1.31 days | 12.46 ± .93 days | 94.78 ± 11.81 |
| All *inter se* matings. | (5) + (3) + (7) | 14.60 ± .57 days | 10.31 ± .40 days | 70.65 ± 3.91 |

2. The similar mating types (P × P and Z × Z) give identical results in mean and variability (having regard to the probable error involved) in respect of duration of life. This agrees with the previous findings for the case of wild type $F_2$ flies.

3. The *inter se* cross mating, P × Z, gives vestigial progeny flies having a significantly *higher* mean duration of life than either of the other two types (P × P, Z × Z). The differences with their probable errors are:

$$\text{For } P \times P,\ 18.50 - 13.10 = 5.40 \pm 1.16 \text{ days}$$
$$\text{For } Z \times Z,\ 18.50 - 13.15 = 5.35 \pm 1.56 \text{ days}$$

While these are not as large as the reverse differences found above in the case of the wild type $F_2$ flies, nevertheless they may be safely regarded, we think, as statistically significant.

The bearing of these differences between the several mating types upon the general problem of the inheritance of duration of life will be discussed further on.

The data regarding duration of life in the $F_2$ individuals produced by back crossing $F_1$ upon the parental types are given in Tables X and XI for wild type flies, and Tables XII and XIII for vestigial flies.

## TABLE X

DEATH AND SURVIVORSHIP DISTRIBUTIONS FOR WILD TYPE $F_2$ FLIES, DERIVED FROM BACK CROSSES OF $F_1$ ON THE PARENTAL STOCKS

| Age in Days | Z × Old Falmouth (8) (Reciprocally) | | | | P × Old Falmouth (4) (Reciprocally) | | | | All Back-crosses of $F_1$ on Wild Type | | Z × Vestigial (2) (Reciprocally) | | | | P × Vestigial (6) (Reciprocally) | | | | All Back-crosses of $F_1$ on Vestigial | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mating 80 | Mating 81 | Total | | Mating 84 | Mating 85 | Total | | Matings 80+81+84+85 | | Mating 78 | Mating 79 | Total | | Mating 82 | Mating 83 | Total | | Matings 78+79+82+83 | |
| | $d_x'$ | $d_x'$ | $d_x'$ | $l_x'$ | $d_x'$ | $d_x'$ | $d_x'$ | $l_x'$ | $d_x'$ | $l_x'$ | $d_x'$ | $d_x'$ | $d_x'$ | $l_x'$ | $d_x'$ | $d_x'$ | $d_x'$ | $l_x'$ | $d_x'$ | $l_x'$ |
| 1– 5..... | 6 | 7 | 13 | 1,000 | — | 2 | 2 | 1,000 | 15 | 1,000 | — | 3 | 3 | 1,000 | — | — | — | 1,000 | 3 | 1,000 |
| 6–11..... | 5 | 28 | 33 | 959 | 1 | 25 | 26 | 995 | 59 | 978 | — | 2 | 2 | 966 | 5 | 3 | 8 | 1,000 | 10 | 986 |
| 12–17..... | 2 | — | 2 | 855 | 4 | 5 | 9 | 923 | 11 | 891 | 5 | 3 | 8 | 943 | 2 | 8 | 10 | 938 | 18 | 940 |
| 18–23..... | 34 | 21 | 55 | 849 | 13 | 11 | 24 | 899 | 79 | 875 | 3 | 3 | 6 | 852 | 13 | 7 | 20 | 860 | 26 | 857 |
| 24–29..... | 16 | 24 | 40 | 675 | 51 | 26 | 77 | 833 | 117 | 760 | 10 | 3 | 13 | 784 | 18 | 6 | 24 | 705 | 37 | 737 |
| 30–35..... | 35 | 19 | 54 | 549 | 23 | 13 | 36 | 622 | 90 | 588 | 15 | 2 | 17 | 636 | 17 | 18 | 35 | 519 | 52 | 567 |
| 36–41..... | 7 | 13 | 20 | 379 | 20 | 15 | 35 | 523 | 55 | 456 | 16 | 4 | 20 | 443 | 3 | 6 | 9 | 248 | 29 | 327 |
| 42–47..... | 10 | 12 | 22 | 315 | 16 | 28 | 44 | 427 | 66 | 375 | 7 | 2 | 9 | 216 | 4 | 4 | 8 | 178 | 17 | 194 |
| 48–53..... | 15 | 13 | 28 | 246 | 11 | 18 | 29 | 307 | 57 | 279 | 4 | 1 | 5 | 114 | 3 | — | 3 | 116 | 8 | 115 |
| 54–59..... | 3 | 28 | 31 | 158 | 16 | 53 | 69 | 227 | 100 | 195 | 3 | 1 | 4 | 57 | 7 | 1 | 8 | 93 | 12 | 78 |
| 60–65..... | 9 | 9 | 18 | 60 | 7 | 4 | 11 | 38 | 29 | 48 | 1 | — | 1 | 11 | 2 | 1 | 3 | 31 | 4 | 23 |
| 66–71..... | — | 1 | 1 | 3 | 1 | 2 | 3 | 8 | 4 | 6 | — | — | — | 0 | 1 | — | 1 | 8 | 1 | 5 |
| 72–77..... | — | — | — | 0 | — | — | — | 0 | — | 0 | — | — | — | — | — | — | — | 0 | — | 0 |
| Totals.... | 142 | 175 | 317 | — | 163 | 202 | 365 | — | 682 | — | 64 | 24 | 88 | — | 75 | 54 | 129 | — | 217 | — |

TABLE XI

BIOMETRIC CONSTANTS FOR DURATION OF LIFE OF WILD TYPE $F_2$ FLIES FROM BACK CROSSES

| Matings | Type | Mean Age at Death | Standard Deviation | Coefficient of Variation |
|---|---|---|---|---|
| Wild ♂ × Z ♀ (80) | (8) | 32.56 ± .83 days | 14.67 ± .59 days | 45.07 ± 2.14 |
| Z ♂ × wild ♀ (81) | (8) | 33.91 ± .93 days | 18.19 ± .66 days | 53.64 ± 2.43 |
| Total Z × wild .... | (8) | 33.30 ± .63 days | 16.72 ± .45 days | 50.20 ± 1.65 |
| Wild ♂ × P ♀ (84) | (4) | 36.57 ± .68 days | 12.85 ± .48 days | 35.13 ± 1.47 |
| P ♂ × wild ♀ (85) | (4) | 38.83 ± .82 days | 17.31 ± .58 days | 44.59 ± 1.77 |
| Total P × wild.... | (4) | 37.82 ± .55 days | 15.52 ± .39 days | 41.03 ± 1.18 |
| Total back cross on wild............ | (8) + (4) | 35.72 ± .42 days | 16.25 ± .30 days | 45.48 ± .99 |
| Vestigial ♂ × Z ♀ (78)............ | (2) | 35.63 ± .91 days | 10.81 ± .64 days | 30.34 ± 1.97 |
| Z ♂ × Vestigial ♀ (79)............ | (2) | 26.56 ± 2.11 days | 15.29 ± 1.49 days | 57.57 ± 7.23 |
| Total Z × Vestigial | (2) | 33.15 ± .92 days | 12.85 ± .65 days | 38.75 ± 2.25 |
| Vestigial ♂ × P ♀ (82)............ | (6) | 32.52 ± 1.09 days | 14.05 ± .77 days | 43.22 ± 2.79 |
| P ♂ × Vestigial ♀ (83)............ | (6) | 29.33 ± 1.05 days | 11.46 ± .74 days | 39.05 ± 2.90 |
| Total P × Vestigial | (6) | 31.19 ± .78 days | 13.12 ± .55 days | 42.08 ± 2.06 |
| Total back cross of vestigial........ | (2) + (6) | 31.98 ± .60 days | 13.05 ± .42 days | 40.80 ± 1.53 |

From Tables X–XIII we note the following points:

1. There is evident a general degradation of mean duration of life in back-cross flies, whether compared with original parents, $F_1$'s or *inter se* $F_2$'s. Thus we have the following system of differences:

Original wild parent — all wild type flies from back crosses of $F_1$ on wild $= 44.26 - 35.72 = 8.54 \pm .61$

Original wild parent — all wild type flies from back crosses of $F_1$ on vestigial $= 44.26 - 31.98 = 12.28 \pm .74$

Original vestigial parent — all vestigial flies from back crosses of $F_1$ on vestigial $= 14.08 - 12.84 = 1.24 \pm .36$

There can be no doubt about a significant lowering of mean duration of life of these back-cross flies as compared with their original progenitors in the P generations. In the worst case (the last) the difference is 3.4 times its probable error.

In the case of $F_1$ flies it is idle to take the differences here because the $F_1$'s are longer lived (as we have already seen) than the wild type original parent. Therefore the differences between $F_1$ and back crosses must of necessity be larger than those we have just examined.

TABLE XII

DEATH AND SURVIVORSHIP DISTRIBUTIONS FOR VESTIGIAL $F_2$ FLIES, DERIVED FROM BACK CROSSES OF $F_1$ ON QUINTUPLE STOCK

| Age in Days | Z × Vestigial (2) (Reciprocally) | | | | P × Vestigial (6) (Reciprocally) | | | | All Back-crosses of $F_1$ on Vestigial | | All $F_1$ ♂ × Vest. ♀ | | All Vestigial ♂ × $F_1$ ♀ | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mating 78 | Mating 79 | Total | | Mating 82 | Mating 83 | Total | | Matings 78+79+82+83 | | Matings 79+83 | | Matings 78+82 | |
| | $d_x'$ | $d_x'$ | $d_x'$ | $l_x'$ | $d_x'$ | $d_x'$ | $d_x'$ | $l_x'$ | $d_x'$ | $l_x'$ | $d_x'$ | $l_x'$ | $d_x'$ | $l_x'$ |
| 1– 2 | 1 | 2 | 3 | 1,000 | 1 | 2 | 3 | 1,000 | 6 | 1,000 | 4 | 1,000 | 2 | 1,000 |
| 3– 5 | 6 | 12 | 18 | 974 | 5 | 14 | 19 | 980 | 37 | 977 | 26 | 968 | 11 | 986 |
| 6– 8 | 3 | 6 | 9 | 819 | 10 | 22 | 32 | 853 | 41 | 838 | 28 | 756 | 13 | 908 |
| 9–11 | 11 | 7 | 18 | 741 | 15 | 16 | 31 | 640 | 49 | 684 | 23 | 532 | 26 | 817 |
| 12–14 | 11 | 6 | 17 | 586 | 19 | 15 | 34 | 433 | 51 | 500 | 21 | 347 | 30 | 634 |
| 15–17 | 15 | 3 | 18 | 440 | 8 | 4 | 12 | 207 | 30 | 308 | 7 | 177 | 23 | 423 |
| 18–20 | 4 | 3 | 7 | 284 | 8 | 4 | 12 | 127 | 19 | 195 | 7 | 121 | 12 | 261 |
| 21–23 | 8 | 2 | 10 | 224 | 2 | 2 | 4 | 47 | 14 | 124 | 4 | 65 | 10 | 176 |
| 24–26 | 5 | 1 | 6 | 138 | 1 | — | 1 | 20 | 7 | 71 | 1 | 32 | 6 | 106 |
| 27–29 | 6 | 1 | 7 | 86 | 1 | — | 1 | 13 | 8 | 45 | 1 | 24 | 7 | 63 |
| 30–32 | 1 | — | 1 | 26 | — | — | — | 7 | 1 | 15 | — | 16 | 1 | 14 |
| 33–35 | 1 | — | 1 | 17 | — | 1 | 1 | 7 | 2 | 11 | 1 | 16 | 1 | 7 |
| 36–38 | — | 1 | 1 | 9 | — | — | — | 0 | 1 | 4 | 1 | 8 | — | 0 |
| 39–41 | — | — | — | 0 | — | — | — | — | — | 0 | — | 0 | — | — |
| Totals | 72 | 44 | 116 | — | 70 | 80 | 150 | — | 266 | — | 124 | — | 142 | — |

TABLE XIII

BIOMETRIC CONSTANTS FOR DURATION OF LIFE OF VESTIGIAL $F_2$ FLIES FROM BACK CROSSES

| Mating | Type | Mean Age at Death | Standard Deviation | Coefficient of Variation |
|---|---|---|---|---|
| Vestigial ♂ × Z ♀ (78) | (2) | 16.47 ± .59 days | 7.41 ± .42 days | 45.01 ± 3.00 |
| Z ♂ × Vestigial ♀ (79) | (2) | 11.41 ± .78 days | 7.64 ± .55 days | 66.92 ± 6.63 |
| Total Z × Vestigial | (2) | 14.55 ± .49 days | 7.89 ± .35 days | 54.22 ± 3.03 |
| Vestigial ♂ × P ♀ (82) | (6) | 12.86 ± .42 days | 5.20 ± .30 days | 40.44 ± 2.66 |
| P ♂ × Vestigial ♀ (83) | (6) | 10.33 ± .41 days | 5.37 ± .29 days | 52.06 ± 3.45 |
| Total P × Vestigial | (6) | 11.51 ± .30 days | 5.44 ± .21 days | 47.30 ± 2.22 |
| Total back crosses on Vestigial | (2) + (6) | 12.84 ± .28 days | 6.79 ± .20 days | 52.91 ± 1.93 |
| Total $F_1$ ♂ × Vestigial ♀ | — | 10.71 ± .38 days | 6.29 ± .27 days | 58.75 ± 3.27 |
| Total Vestigial ♂ × $F_1$ ♀ | — | 14.69 ± .38 days | 6.67 ± .27 days | 45.38 ± 2.16 |

For the $F_2$'s from *inter se* matings of $F_1$ we have the following:

$F_2$ (from P × P) wild type — wild type from back cross P × wild $= 46.34 - 37.82 = 8.52 \pm .91$

$F_2$ (from Z × Z) wild type — wild type from back cross Z × wild $= 46.01 - 33.30 = 12.71 \pm .96$

$F_2$ (from P × Z) wild type — wild type from all back crosses on wild $= 37.66 - 35.72 = 1.94 \pm .77$

$F_2$ (from P × P) wild type — wild type from back cross P × vestigial $= 46.34 - 31.19 = 15.15 \pm 1.07$

$F_2$ (from P × Z) wild type — wild type from all back crosses on vestigial $= 46.01 - 33.15 = 12.86 \pm 1.17$

$F_2$ (from P × Z) wild type — wild type from all back crosses on vestigial $= 37.66 - 31.98 = 5.68 \pm .88$

Thus it is clear that the wild type $F_2$ flies from back crosses of $F_1$ upon either original parent have a significantly lower mean duration of life than do the $F_2$ flies from *inter se* matings of $F_1$. The only exception to this rule is found in the case of the $F_2$ from the P × Z matings, when compared with all back crosses upon wild. This difference is less than three times its probable error.

Turning now to vestigials we have:

$F_2$ (from P × P) vestigial — vestigial from back cross P × vestigial = 13.10 — 11.51 = 1.59 ± .54
$F_2$ (from Z × Z) vestigial — vestigial from back cross Z × vestigial = 13.15 — 14.55 = — 1.40 ± 1.40
$F_2$ (from P × Z) vestigial — vestigial from all back crosses on vestigial = 18.50 — 12.84 = 5.66 ± .89

Here the only difference which is significant is the last, which involves the P × Z $F_1$ flies. Everywhere this group gives an aberrant result.

2. There are certain definite and orderly differences in mean duration of life between the flies from the two moieties of otherwise identical reciprocal back crosses, and also between the flies coming from back crosses involving the two sorts of $F_1$'s, namely P and Z. These differences are as follows:

WILD TYPE FLIES

(Wild ♂ × Z ♀) — (Wild ♂ × P ♀) = 32.56 — 36.57 = — 4.01 ± 1.07
(Z ♂ × Wild ♀) — (P ♂ × Wild ♀) = 33.91 — 38.83 = — 4.92 ± 1.24
(Vest. ♂ × Z ♀) — (Vest. ♂ × P ♀) = 35.63 — 32.52 = + 3.11 ± 1.42
(Z ♂ × vest. ♀) — (P ♂ × vest. ♀) = 26.56 — 29.33 = — 2.77 ± 2.36

VESTIGIAL FLIES

(Vest. ♂ × Z ♀) — (Vest. ♂ × P ♀) = 16.47 — 12.86 = + 3.61 ± .72
(Z ♂ × vest. ♀) — (P ♂ × vest. ♀) = 11.41 — 10.33 = + 1.08 ± .88

From these differences it appears that when the back-cross mating is such as to produce only wild type flies the offspring are significantly longer lived when the $F_1$ parent is of P origin than when it is of Z origin. The reverse *appears* to be true when the mating is of the sort to produce both wild and vestigial types in the offspring, though most of the series here are unfortunately too short to give statistically significant differences.

The differences between reciprocal matings are as follows:

WILD TYPE FLIES

(Wild ♂ × Z ♀) — (Z ♂ × wild ♀) = 32.56 — 33.91 = — 1.35 ± 1.25
(Wild ♂ × P ♀) — (P ♂ × wild ♀) = 36.57 — 38.83 = — 2.26 ± 1.07
(Vest. ♂ × Z ♀) — (Z ♂ × vest. ♀) = 35.63 — 26.56 = + 9.07 ± 2.30
(Vest. ♂ × P ♀) — (P ♂ × vest. ♀) = 32.52 — 29.33 = + 3.19 ± 1.51

VESTIGIAL FLIES

(Vest. ♂ × Z ♀) — (Z ♂ × vest. ♀) = 16.47 — 11.41 = + 5.06 ± .98
(Vest. ♂ × P ♀) — (P ♂ × vest. ♀) = 12.86 — 10.33 = + 2.53 ± .49

From these data it appears that in back crosses of $F_1$ on wild the offspring tend to be *longer* lived (though because of the shortness of the series neither difference is significant) when the *mother* is pure wild: in back crosses of $F_1$ on vestigial, the offspring, whether wild or vestigial, are *shorter* lived when the *mother* is pure *vestigial.* All the differences but one are clearly significant, and that one is probably so. There thus appears here a definite matroclinal tendency relative to the inheritance of duration of life.

## $F_3$ GENERATION

The matings made to produce $F_3$ flies were few in number, as is shown in Table II, and covered only a small fraction of the possibilities. In Table XIV are given the Mendelian results, relative to the segregation of normal and vestigial wing, for all the matings it was possible to use. The other matings indicated in Table II could not be used in the analysis, because they were mass matings in which a fly might be either heterozygous or pure dominant, and as a matter of fact some were heterozygous, as indicated by the results, in the case of the three matings not included in Table XIV.

Because of interest in their apparently aberrant behavior, already brought out, attention was confined in making up the matings for $F_3$ to the $F_2$ produce of P × Z matings.

It will be seen from Table XIV that in every case of matings involving vestigial $F_2$ females (which includes all matings in the table except the last) there is an *excess of vestigial flies* in the offspring, over what would be expected on Mendelian theory. The discrepancies are certainly significant in the totals, and also for two out of the four separate matings. It will be recalled that Table V shows an excess of vestigials from the back crosses of $F_1$ on the parent stocks.

Tables XV–XVIII inclusive give the $F_3$ results as to duration of life.

## TABLE XIV

MENDELIAN SEGREGATION IN F$_3$ OF NORMAL AND VESTIGIAL WINGS, TABULATED BY SEPARATE MATINGS

| Mating Type | Number of F$_3$ Flies with Wings | | | Probable Error | Deviation | Probable Times of Occurrence of Such a Deviation in 100 Trials | Mating No. |
|---|---|---|---|---|---|---|---|
| | Normal | Vestigial | Total | | P.E. Dev. | | |
| *Vestigial* ♀ ♀ | | | | | | | |
| (54) Z ♂ × D (76) ♀ | 76 | 121 | 197 | | | | 86 |
| *Expected* | *98.5* | *98.5* | *197* | ±4.73 | 4.8 | .12 | |
| (54) Z ♂ × D (77) ♀ | 67 | 76 | 143 | | | | 90 |
| *Expected* | *71.5* | *71.5* | *143* | ±4.03 | 1.1 | 45.81 | |
| (54) Total | 143 | 197 | 340 | | | | 86+90 |
| *Expected* | *170* | *170* | *340* | ±6.22 | 4.3 | .37 | |
| (52) P ♂ × D (76) ♀ | 95 | 107 | 202 | | | | 88 |
| *Expected* | *101* | *101* | *202* | ±4.79 | 1.3 | 38.06 | |
| (52) P ♂ × D (77) ♀ | 63 | 119 | 182 | | | | 92 |
| *Expected* | *91* | *91* | *182* | ±4.55 | 6.2 | .005 | |
| (52) Total | 158 | 226 | 384 | | | | 88+92 |
| *Expected* | *192* | *192* | *384* | ±6.61 | 5.1 | .07 | |
| Wild type ♀ ♀ | | | | | | | |
| (52) P ♂ × D (76) ♀ | 175 | 0 | 175 | | | | 89 |
| *Expected* | *175* | *0* | *175* | — | — | — | — |

## TABLE XV

DEATH AND SURVIVORSHIP DISTRIBUTIONS FOR WILD TYPE F$_3$ FLIES

| Age in Days | Z F$_1$ ♂ × Vestigial D F$_2$ ♀ | | | | P F$_1$ ♂ × Vestigial D F$_2$ ♀ | | | | P F$_1$ ♂ × Wild Type D F$_2$ ♀ | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Mating 86 | Mating 90 | Total | | Mating 88 | Mating 92 | Total | | Mating 89 | |
| | $d_x'$ | $d_x'$ | $d_x'$ | $l_x'$ | $d_x'$ | $d_x'$ | $d_x'$ | $l_x'$ | $d_x'$ | $l_x'$ |
| 1–5 | 1 | 1 | 2 | 1,000 | 11 | 3 | 14 | 1,000 | 2 | 1,000 |
| 6–11 | 5 | 2 | 7 | 986 | 6 | 8 | 14 | 911 | 6 | 989 |
| 12–17 | 9 | 13 | 22 | 937 | 10 | 6 | 16 | 823 | 26 | 954 |
| 18–23 | 18 | 24 | 42 | 783 | 21 | 9 | 30 | 722 | 35 | 806 |
| 24–29 | 5 | 11 | 16 | 490 | 13 | 4 | 17 | 532 | 12 | 606 |
| 30–35 | 5 | 9 | 14 | 378 | 5 | 6 | 11 | 424 | 23 | 537 |
| 36–41 | 6 | 2 | 8 | 280 | 6 | 6 | 12 | 354 | 14 | 406 |
| 42–47 | 6 | 1 | 7 | 224 | 6 | 4 | 10 | 278 | 29 | 326 |
| 48–53 | 15 | 2 | 17 | 175 | 14 | 12 | 26 | 215 | 18 | 160 |
| 54–59 | 6 | 2 | 8 | 56 | 3 | 5 | 8 | 51 | 10 | 57 |
| 60–65 | — | — | — | 0 | — | — | — | 0 | — | 0 |
| 66–71 | — | — | — | — | — | — | — | — | — | — |
| Totals | 76 | 67 | 143 | — | 95 | 63 | 158 | — | 175 | — |

## TABLE XVI

### BIOMETRIC CONSTANTS FOR DURATION OF LIFE OF WILD TYPE $F_2$ FLIES

| Mating | Type | Mean Age at Death | Standard Deviation | Coefficient of Variation |
|---|---|---|---|---|
| Z $F_1$ ♂ × Vest. $D_{76}$ $F_2$ ♀ (86). | (54) | 32.53 ±1.22 | 15.74 ± .86 | 48.37 ±3.21 |
| Z $F_1$ ♂ × Vest. $D_{77}$ $F_2$ ♀ (90). | (54) | 24.68 ± .87 | 10.55 ± .61 | 42.80 ±2.92 |
| Total Z $F_1$ ♂ × Vest. D ♀ ... | (54) | 28.85 ± .80 | 14.11 ± .56 | 48.91 ±2.37 |
| P $F_1$ ♂ × Vest. $D_{76}$ $F_2$ ♀ (88). | (52) | 27.25 ±1.10 | 15.88 ± .78 | 58.29 ±3.70 |
| P $F_1$ ♂ × Vest. $D_{77}$ $F_2$ ♀ (92). | (52) | 31.40 ±1.44 | 16.90 ±1.02 | 53.83 ±4.07 |
| Total P $F_1$ ♂ × Vest. D ♀ ... | (52) | 28.90 ± .88 | 16.42 ± .62 | 56.82 ±2.77 |
| P $F_1$ ♂ × Wild type $D_{76}$ $F_2$ ♀ (89) .................... | (52) | 32.05 ± .72 | 14.18 ± .51 | 44.26 ±1.88 |

## TABLE XVII

### DEATH AND SURVIVORSHIP DISTRIBUTIONS FOR VESTIGIAL $F_2$ FLIES

| Age in Days | Z $F_1$ ♂ × Vestigial D $F_2$ ♀ | | | | P $F_1$ ♂ × Vestigial D $F_2$ ♀ | | | |
|---|---|---|---|---|---|---|---|---|
| | Mating 86 | Mating 90 | Total | | Mating 88 | Mating 92 | Total | |
| | $d_x'$ | $d_x'$ | $d_x'$ | $l_x'$ | $d_x'$ | $d_x'$ | $d_x'$ | $l_x'$ |
| 1– 2....... | 45 | 12 | 57 | 1,000 | 22 | 21 | 43 | 1,000 |
| 3– 5....... | 50 | 25 | 75 | 711 | 16 | 27 | 43 | 810 |
| 6– 8....... | 7 | 21 | 28 | 330 | 12 | 19 | 31 | 619 |
| 9–11....... | 9 | 7 | 16 | 188 | 14 | 15 | 29 | 482 |
| 12–14....... | 5 | 4 | 9 | 107 | 22 | 34 | 56 | 354 |
| 15–17....... | 1 | 7 | 8 | 61 | 16 | 3 | 19 | 106 |
| 18–20....... | 2 | — | 2 | 20 | 2 | — | 2 | 22 |
| 21–23....... | — | — | — | 10 | — | — | — | 13 |
| 24–26....... | 1 | — | 1 | 10 | — | — | — | 13 |
| 27–29....... | 1 | — | 1 | 5 | — | — | — | 13 |
| 30–32....... | — | — | — | 0 | — | — | — | 13 |
| 33–35....... | — | — | — | — | 1 | — | 1 | 13 |
| 36–38....... | — | — | — | — | 2 | — | 2 | 9 |
| Totals...... | 121 | 76 | 197 | — | 107 | 119 | 226 | — |

## TABLE XVIII

### BIOMETRIC CONSTANTS FOR DURATION OF LIFE OF VESTIGIAL $F_2$ FLIES

| Mating | Type | Mean Age at Death | Standard Deviation | Coefficient of Variation |
|---|---|---|---|---|
| Z $F_1$ ♂ × Vest. $D_{76}$ $F_2$ ♀ (86). | (54) | 5.28 ±.28 | 4.64 ±.20 | 87.95 ±6.09 |
| Z $F_1$ ♂ × Vest. $D_{77}$ $F_2$ ♀ (90). | (54) | 7.07 ±.33 | 4.21 ±.23 | 59.60 ±4.26 |
| Total Z $F_1$ × Vest. D ♀ ...... | (54) | 5.97 ±.22 | 4.57 ±.16 | 76.49 ±3.83 |
| P $F_1$ ♂ × Vest. $D_{76}$ $F_2$ ♀ (88). | (52) | 9.93 ±.45 | 6.98 ±.32 | 70.26 ±4.57 |
| P $F_1$ ♂ × Vest. $D_{77}$ $F_2$ ♀ (92). | (52) | 8.17 ±.28 | 4.52 ±.20 | 55.29 ±3.07 |
| Total P $F_1$ ♂ × Vest. D ♀ ... | (52) | 9.00 ±.26 | 5.88 ±.19 | 65.30 ±2.82 |

The first point which will be noted from these Tables XV–XVIII is the still further marked degradation in duration of life of $F_3$ flies, as compared with those of earlier generations. None of the means approach in value the original parental stocks, and are even well below, taken as a whole, the $F_2$ flies from back crosses.

Another result is the system of differences, in the main significant, in duration of life according to whether the $F_2$ vestigial females used were from mating 76 or mating 77. $D_{76}$ females came from Z ♂ × P ♀, and $D_{77}$ females came from P ♂ × Z ♀. Now, when a $D_{76}$ ♀ was mated back to Z ♂, the resulting wild type flies were longer lived and the vestigials were shorter lived than when a $D_{77}$ female was mated to a Z ♂. When these same two sorts of females were mated to a P ♂ the offspring of the $D_{77}$ females were longer lived if normal winged and shorter lived if vestigial winged than the offspring of the $D_{76}$ females.

In the one mating (89) which enables a comparison of $D_{76}$ wild type and a $D_{76}$ vestigial each mated to the same type of male (P), the resulting wild type progeny are longer lived from the wild type mother. The difference 4.80 ± 1.31 days is almost certainly significant.

## THE EFFECT OF ABSENCE OF WINGS ON DURATION OF LIFE

It can not fail to occur to one that perhaps the reason why vestigial winged flies are invariably short lived is merely and directly physiological, arising because such a fly has no *functional* wings and therefore can not fly, but has its activity confined to walking and jumping. Stated in extreme forms, the idea would be that so far as inherent constitutional factors influencing duration of life are concerned Quintuple and wild stocks are on the same footing, but because Quintuple has no functional wings it is physiologically unable so to conduct its life as to realize its constitutional potentialities in respect of longevity.

It is possible experimentally to test this idea, in part at least. Suppose in a large number of wild type flies immediately after emergence the wings are cut off close to the body. Since they do not regenerate these flies must then go through life wingless. If then a duration of life experiment is carried through with them, and a life curve constructed, will this curve be like that for Quintuple flies, or will it be like that for normal wild flies? Or, put in another way, what difference in the distribution of mortality of *Drosophila* does the presence or absence of wings make in a purely physiological, somatic sense?

This experiment we have carried out on a large scale twice. Unfortunately we can give here the result only of the second of these investigations, because in the case of the first series all the surviving flies were destroyed when rather more than half way through the life curve, owing to the accidental misbehavior of the regulating apparatus of the incubator in which they were. The results, however, so far as they went were in entire agreement with those here presented.

The flies in this experiment emerged April 16–19, 1922, from 25 mass matings (2 pairs each) Old Falmouth stock, line 107, generation 26. Progeny were taken from the mating bottles at 24-hour intervals and etherized. Only the flies whose wings were fully expanded and dried were used, in either experimental or control group. With fine scissors both wings were clipped off as close to the thorax as possible, care being taken to avoid injury to the halteres. The experimental and control bottles—with 30 flies in each bottle—were made up alternately to distribute the flies at random. Both sets were then put through a standard duration of life test at 25° C. in the usual way in which all our work is done, with the results shown in Tables XIX and XX and Fig. 4.

From the results it is evident that surgical removal of the normal wings of wild type flies at the time of emergence somewhat shortens duration of life, but to no such

TABLE XIX

Death and Survivorship Distributions for Wild Type Flies (*a*) with Wings Surgically Removed, and (*b*) with Normal Wings

| Age in Days | Normal Wings | | Wings Removed | |
|---|---|---|---|---|
| | $d_x'$ | $l_x'$ | $d_x'$ | $l_x'$ |
| 1– 3 | 5 | 1,000 | 4 | 1,000 |
| 4– 6 | 2 | 990 | 10 | 992 |
| 7– 9 | 4 | 986 | 20 | 973 |
| 10–12 | 4 | 979 | 9 | 934 |
| 13–15 | 9 | 971 | 34 | 917 |
| 16–18 | 12 | 953 | 30 | 852 |
| 19–21 | 22 | 930 | 45 | 794 |
| 22–24 | 22 | 887 | 38 | 707 |
| 25–27 | 17 | 844 | 26 | 634 |
| 28–30 | 33 | 811 | 37 | 584 |
| 31–33 | 21 | 747 | 21 | 513 |
| 34–36 | 20 | 706 | 22 | 472 |
| 37–39 | 26 | 667 | 19 | 430 |
| 40–42 | 33 | 618 | 21 | 393 |
| 43–45 | 34 | 553 | 26 | 353 |
| 46–48 | 34 | 486 | 24 | 303 |
| 49–51 | 33 | 420 | 20 | 256 |
| 52–54 | 42 | 356 | 32 | 218 |
| 55–57 | 64 | 274 | 28 | 156 |
| 58–60 | 25 | 150 | 27 | 102 |
| 61–63 | 20 | 101 | 11 | 50 |
| 64–66 | 12 | 62 | 9 | 29 |
| 67–69 | 5 | 39 | 1 | 12 |
| 70–72 | 8 | 29 | 3 | 10 |
| 73–75 | 2 | 14 | 1 | 4 |
| 76–78 | 4 | 10 | 1 | 2 |
| 79–81 | — | 2 | — | 0 |
| 82–84 | 1 | 2 | — | 0 |
| 85–87 | — | 0 | — | 0 |
| Totals | 514 | — | 519 | — |

TABLE XX

Biometric Constants for Duration of Life in Wild Type Flies (*a*) with Wings Surgically Removed, and (*b*) with Normal Wings

| Group | Mean Duration of Life | Standard Deviation | Coefficient of Variation |
|---|---|---|---|
| Wings removed | 34.56±.50 days | 17.01±.36 days | 49.23±1.26 |
| Normal wings | 43.26±.47 days | 15.69±.33 days | 36.27± .86 |

extent as would be required to account for the normal difference between wild and Quintuple stocks in this respect. The differences between clipped and unclipped groups are significant in comparison with their probable errors, but the difference between the means is only about one fourth of the difference between wild and Quintuple means.

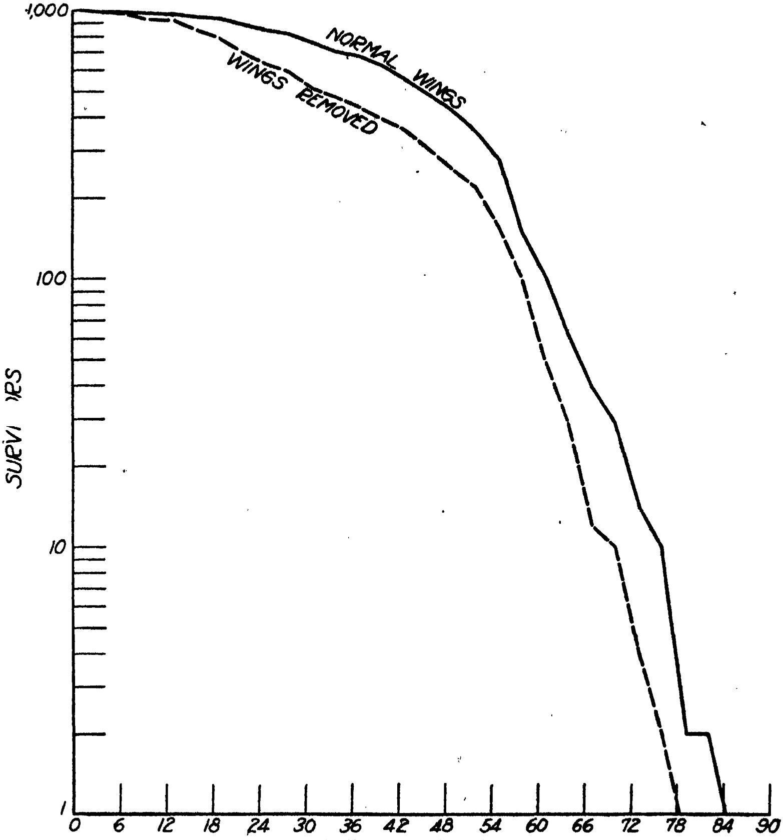


FIG. 4. Survivorship lines for normal wild type flies (solid lines) and flies of same stock with wings removed at emergence (broken lines).

It may be safely concluded that the difference between wild and Quintuple stocks in respect of duration of life is not solely due to the fact that the Quintuple have no functional wings while the wild do. One perhaps could reasonably have concluded this on general grounds, but it seemed well to have an experimental proof. Certainly a considerable part of the difference between clipped and unclipped shown in the data, and perhaps nearly all of it, is due to the unavoidable and unperceived gross injury to the fly at the time of the operation. Three times as many clipped as unclipped died during the first 10 days of life. No effort was made at the operation to do anything to the wing stumps to prevent loss of body fluids. We have in the results the maximum effect of *both* absence of wings throughout life, and a rather rough major surgical operation at the start of life. If the second of these two factors could be eliminated and leave the first by itself alone, it is probable that the two curves of Fig. 4 would be insignificantly different from each other.

## *Discussion of Results*

So far we have studiously avoided any discussion of the meaning of the results, desiring to present the objective facts separated clearly from any interpretation of them. We wish now to enter upon a brief discussion of the meaning of what we have found, prefacing our remarks in this direction by the statement that we regard this investigation as in no way final, but rather as preliminary to a series (probably long) of experimental studies which must be made before anything like a complete understanding of the mechanism of inheritance of duration of life in *Drosophila* will be possible.

For convenience in discussion we have summarized all our experiments in the form of pedigree diagrams in Figs. 5–17, entering beside each designation of the type of fly the mean duration of life of that group to the nearest whole number of days.

With the data before us we may point out the broad results of the investigation. These seem to us to be:

1. Duration of life behaves in the $F_1$, $F_2$ and a part of the possible $F_3$ offspring from reciprocal crosses of short-lived and long-lived strains of *Drosophila* as any character of the organism would be expected to behave if it were inherited in a Mendelian manner. There is a

somewhat higher duration of life in $F_1$ than in either of the parent stocks (effect of heterosis). There is a clear-cut segregation of long-lived and short-lived groups in subsequent generations.

2. In its genetic behavior duration of life is completely and invariably associated with certain morphological characteristics of the flies, in the sense that no vestigial-winged fly has ever been found to be long-lived, and no group of normal-winged flies have ever been found to have a life curve even approaching in form that which is characteristic of vestigial-winged flies.

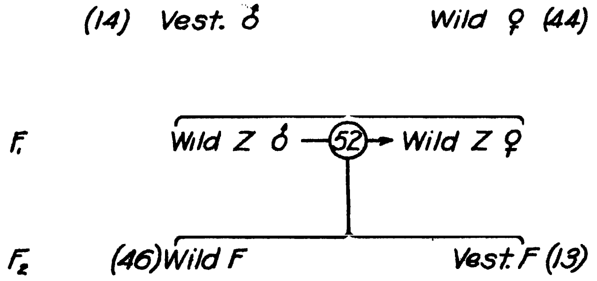


FIG. 5

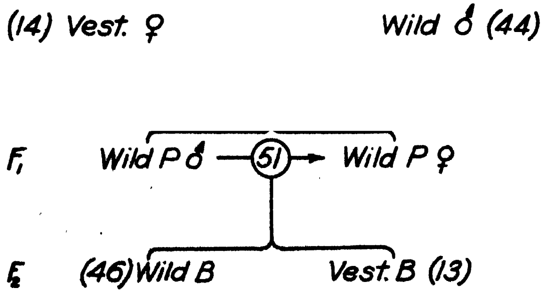


FIG. 6

There are three possible interpretations of these results which suggest themselves in the light of our present knowledge of, and viewpoint about, genetic phenomena in general. These are:

1. It may be assumed that duration of life is deter-

mined by a single Mendelian gene, completely or perfectly linked to the gene for vestigial, so that crossing over never occurs between the former and the latter.

2. It may be assumed that duration of life is a character, like body size, controlled by *n* factors, each of which Mendelizes. This postulates what amounts to a whole flock of genes for viability in a graded series, such that the effect of each translates itself into actuality at varying points in the entire span of imaginal life.[2]

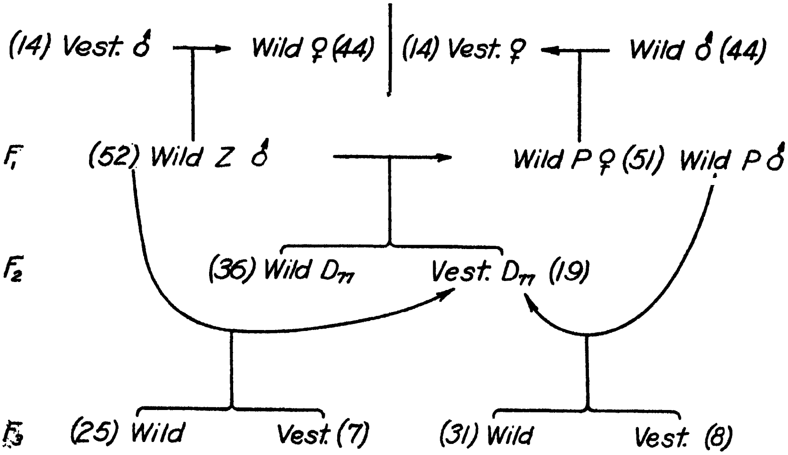


FIG. 7

3. *It may be assumed that duration of life is not in and of itself a separate and different character of the organism, but instead is simply the expression in time of the organization of the body,* which organization may be regarded as physico-chemical, structural, physiological or functional, depending upon which of the aspects of organization we may at the time be emphasizing.

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[2] Obviously if we are to have viability or lethal genes at all there is no reason why we should suppose them confined to embryonic, or larval, or pupal stages of the life history. A gene that kills at age 50 days is just as easily conceived, and for all we know just as probable *a priori,* as one that kills 2-day-old larvæ. Presumably what a lethal gene means biologically is merely that it determines an organization of the body such that viability ceases (or put the other way about, that the individual cannot go on living) after that organization (structural or functional) has attained its full somatic development.

Of these alternative hypotheses the first may be dismissed at once for two reasons, first because it is inherently improbable biologically, and second because, as will be demonstrated in the next following paper in this series, the same kind of evidence as that adduced in this paper can be brought forward to indicate a separate gene for duration of life completely linked to the genes for each one of a whole series of morphological characters, such as eye color and the like.

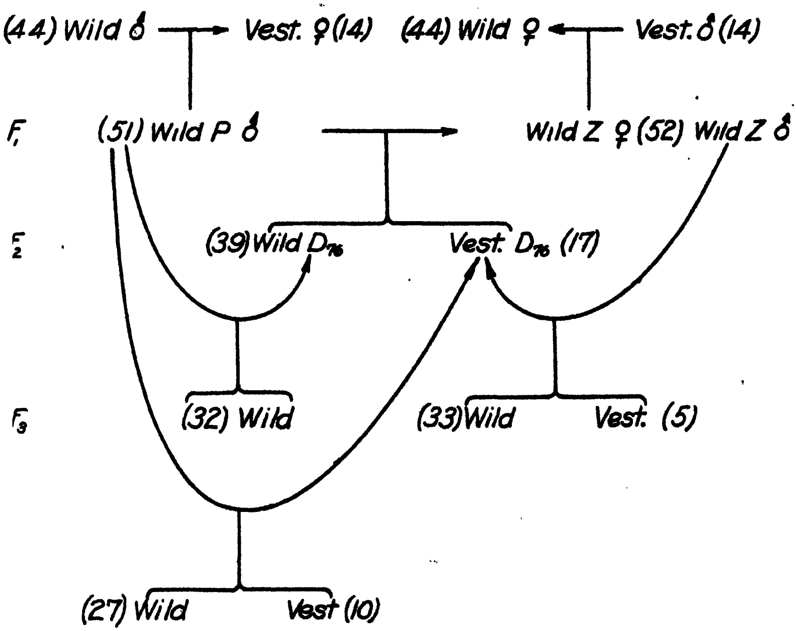

FIG. 8

Regarding the second hypothesis it may be said to violate the logical principle *Entia non sunt multiplicanda præter necessitatem.* For why should we postulate a series of *special* genes for duration of life, each necessarily (because of the observed facts) completely associated or linked with genes for morphological characters. To do so seems to us to serve no useful purpose.

With the third hypothesis, which has been discussed by one of us elsewhere (52), the existing knowledge seems to be in general in entire accord. It means that in a strict sense we can not speak of the inheritance of duration of life any more properly than we can speak of the inheritance of tuberculosis.[3]

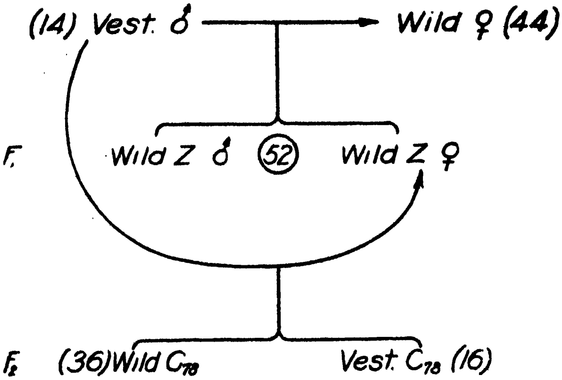

FIG. 9

What is inherited in both cases is not the thing itself, but the bodily organization, of which duration of life, on the one hand, and the disease tuberculosis, on the other hand, are in part the manifestations. In short what is

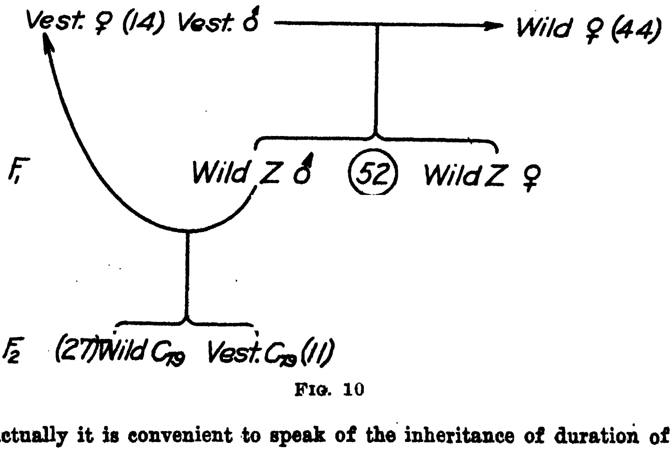

FIG. 10

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[3] Actually it is convenient to speak of the inheritance of duration of life, just as it is to say that tuberculosis is in some degree inherited. And no harm can be done by such usage of words, provided one understands that it is merely a verbal economy, to save the use of a longer and more awkward phrase.

inherited is the *diathesis* for longevity, not longevity itself. Put in another way, what this view of the matter says is that if the duration of an individual's life is an implicit function of the individual's organization or constitution (a purely physical thing fundamentally) which is inherited, it follows that duration of life will behave exactly as though it were itself inherited. It then directly follows that, from the standpoint of methodology, we may by a genetic study of duration of life get valuable knowledge as to the mode or form of the functional relationship between physical organization and duration of life, which in fact is thus perceived from a new angle to be the fundamental problem involving duration of life.

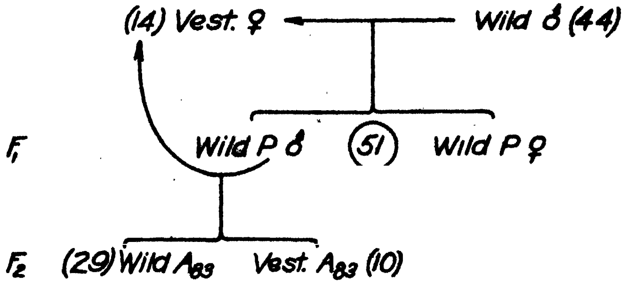

FIG. 11

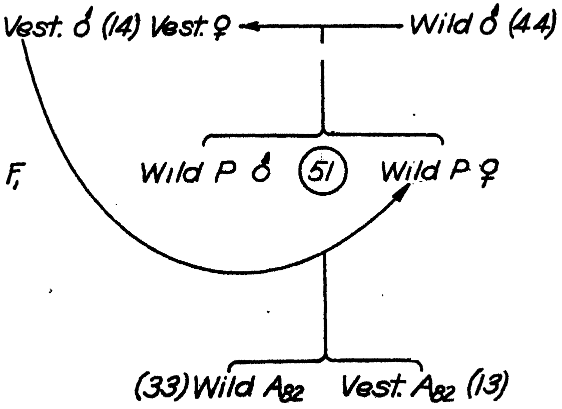

FIG. 12

This means that in the present series of experiments we have demonstrated that the gene for vestigial, besides affecting the form, size and general functional organization of the wings of *Drosophila, also* influences, in and through its effects on the whole organization of every fly in which it is present, the duration of life of that fly. We have measured with considerable exactness and manifoldness what the quantitative effect of this gene is upon duration of life (and, of course, at the same time the effect of its allelomorph the gene for normal wing).

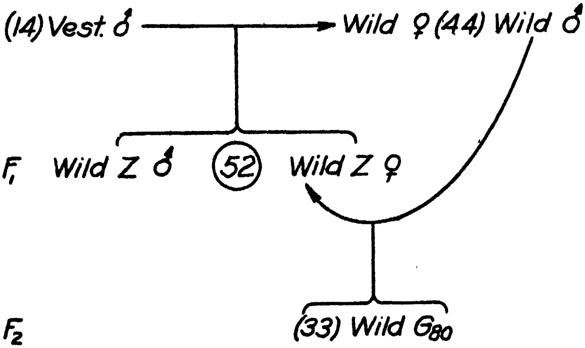

FIG. 13

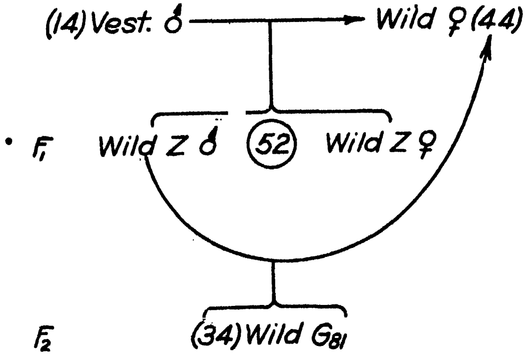

FIG. 14

This view of the case seems to us to be in accord with the best current opinion as to the biological meaning of mutant genes generally. Thus Morgan (9, pp. 238–239) says:

> If we examine almost any mutant race, such as the race of white-eyed *Drosophila*, we find that the white eye is only one of the characteristics that such a mutant race shows. The productivity of the individual is also much affected, and the viability is lower than in the wild fly. All of these peculiarities are found whenever the white eye emerges from a cross and are not separable from the white-eyed condition. It follows that whatever it is in the germ-plasm that produces white eyes also produces other modifications as well, and modifies not only such "superficial" things as color, but also such "fundamental" things as productivity and viability. Many examples of this manifold effect are known to students of heredity.
>
> It is perhaps not going too far to say that any change in the germ-plasm may produce many kinds of effects on the body. Clearly then the character that we choose to follow in any case is only the most conspicuous or (for purposes of identification) the most striking or convenient modification that is produced. Since, however, these effects always go together, and can be explained by the assumption of a single unit difference in the germ-plasm, the particular difference in the germ-plasm is more significant than the character chosen as its index.

The general view as to the mechanism through which duration of life behaves as an inherited character which is here tentatively adopted has been discussed in more

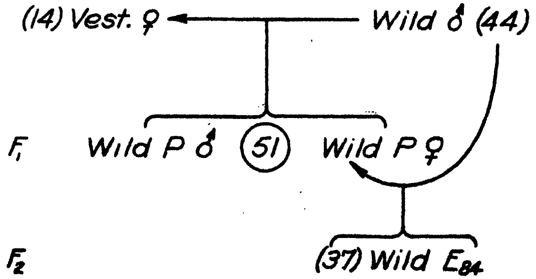

FIG. 15

detail by Pearl at various points in "The Biology of Death" (52). Thus it is there suggested (p. 212) that "what heredity does in relation to duration of life is chiefly to determine, within fairly narrow limits, the total energy output which the individual can exhibit in its life time. This limitation is directly brought about presumably through two general factors: viz., (*a*) the kind or quality of material of which this particular vital machine is built, and (*b*) the manner in which the parts are put together or assembled."

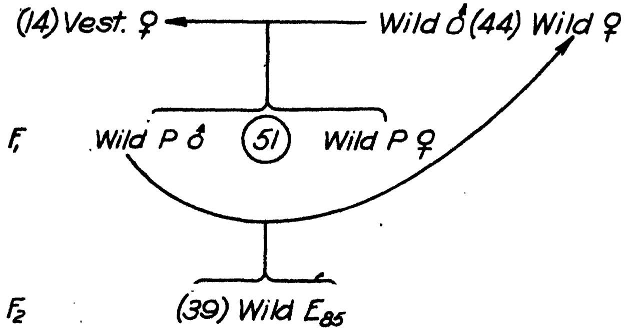

FIG. 16

In this statement (*a*) and (*b*) are equivalent to what is here, in more general terms, called "organization."

To come now to details of the present investigation there are a number of points for which we have no present explanation to offer. The chief of these are:

1. The significantly aberrant Mendelian ratios of vestigial.

2. The peculiar differences in duration of life, apparently associated with these departures from Mendelian expectation of vestigial. We refer to such matters as the divergent results of Z × P as compared with other *inter se* matings of $F_1$ to produce $F_2$; the peculiar behavior of duration of life in back crosses: the failure of reciprocal matings to give identical results, though all morphological mutants dealt with have their location in the second chromosome.

3. The steady degradation in mean duration of life after $F_1$.

The present material is inadequate to the solution of these difficulties. It has certain defects which contribute heavily to this inadequacy. In the first place Quintuple carries 5 different mutations each one of which has *some* influence on duration of life, as will be demonstrated in the next following paper in this series. We took account of but one of these morphological characters (namely vestigial) in this study. In the second place the material is not large enough in mass to deal adequately with the kind of deviations from expectation that appeared. In subsequent investigations we hope to remedy these defects. In the meantime the present study has fulfilled, we believe, the highest pragmatic test of any genetic inquiry. Namely, we are now in a position to predict what the duration of life of a progeny group of *Drosophila* will be, from a knowledge of the duration of life of the parents.

## SUMMARY

In this study, involving the determination of the duration of life of 5,415 individual flies, a cross was made between a long-lived stock of *Drosophila* (Old Falmouth, wild type) and a short-lived stock (Quintuple). In the $F_1$ generations the progeny were somewhat longer lived than either parent stock. In $F_2$ there was a definite and clear-cut segregation in respect of duration of life, long-lived and short-lived groups reappearing, with virtually identical mean duration of life to those of the original parent stocks. In its genetic behavior duration of life was found to be completely and invariably associated with certain morphological characteristics of the organism, in the sense that no vestigial-winged fly has ever been found, in the entire experience of the laboratory, to be long-lived, and no group of normal-winged flies has ever been found to have a life curve even approaching in form that which is characteristic of vestigial-winged flies. The probable meaning of these results, in relation to genetic phenomena in general, is discussed.

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# GEOGRAPHICAL DISTRIBUTION

## II

SYMPOSIUM ON GEOGRAPHICAL DISTRIBUTION PRESENTED BEFORE A JOINT SESSION OF THE AMERICAN SOCIETY OF ZOOLOGISTS, THE AMERICAN SOCIETY OF NATURALISTS AND THE ECOLOGICAL SOCIETY OF AMERICA*

# THE FISHES OF THE PACIFIC SLOPE OF SOUTH AMERICA AND THE BEARING OF THEIR DISTRIBUTION ON THE HISTORY OF THE DEVELOPMENT OF THE TOPOGRAPHY OF PERU, ECUADOR AND WESTERN COLOMBIA[1]

PROFESSOR CARL H. EIGENMANN

UNIVERSITY OF INDIANA

THE freshwater fish fauna of South America is the richest in the world, both in the actual number of species and the relative number of autochthonous genera and families. All but a few strays and a few species in the extreme southern end of the continent are peculiar to South America.

This fauna developed with the present form and topography of the continent. It is a mistake to assume that the continent, or any part of it, was formed and became planted later. The development of the fauna was and is intimately associated with the development of both the shape and topography of the continent.

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* Cambridge meeting, December 29, 1922. The first four papers were printed in the issue of THE AMERICAN NATURALIST for March–April.

[1] Contribution from the Zoological Laboratory of Indiana University. No. 184.

In "The Freshwater Fishes of Patagonia and an Examination of the Archiplata-Archhelenis Theory,"[2] I reviewed the knowledge of the distribution of the freshwater fishes of South America and outlined a program for future work. I have been at work on the program outlined ever since—in fact for some time before 1909, the date of publication, for the plan was made several years earlier. An outline for work in Panama and western Colombia was published in 1905[3] and an abstract of the whole scheme in 1906.[4]

The present paper reviews the work and presents some of the general conclusions reached from the work in Panama, western Colombia and the Pacific slopes of Ecuador, Peru and Chili.

The late Dr. S. E. Meek and S. F. Hildebrand did the field work in Panama. Their volume, "The Fishes of the Fresh Waters of Panama," was published in 1916.[5] (Their volume on the marine fishes is going through the press.)

I travelled in the early part of 1912 from Panama to Cartagena, Colombia, went up the Magdalena and to Bogota, then westward to the coast at Buenaventura. Then I went up the San Juan, crossed the low divide to the Atrato and descended that stream to its mouth.[6] In 1913, Messrs. Arthur Henn and Charles Wilson (The Landon-Fisher Expedition) collected in the Patia in southwestern Colombia and in the lower San Juan. Later Mr. Wilson came over the divide to the Atrato and supplemented my work in that stream while Mr. Henn (The Landon Expedition) went to western Ecuador and examined the Guayas basin and the plateaus of Ecuador.[7]

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[2] *Reports of the Princeton University Expeditions to Patagonia*, III, 1909.

[3] *Science*, N. S., XXII, pp. 1–20, July, 1905.

[4] *Popular Science Monthly*, June, 1906, pp. 515–530.

[5] *Field Museum Publications*, Zool. Ser. X, No. 15, pp. 1–63 and 1–252, 1916.

[6] Some results from an ichthyological reconnaissance of Colombia, South America, *Indiana University Studies* No. 16, particularly pages 1–9, Dec., 1912.

[7] "Indiana University Expeditions to Northwestern South America," *Science*, N. S., XL, pp. 602–606, 1914.

In 1918 and 19, during the Irwin Expedition,[8] I examined some of the Pacific slope streams of Peru, and Chili, from Paita, about 5° S. to Puerto Montt at 41° 28′ S.

During the Centennial Expedition of Indiana University[9] Dr. W. R. Allen made additional collections in the Rio Rimac.

Lastly, Mr. N. E. Pearson, a member of the Mulford Expedition, 1921, made collections in the Rio Tambo, southern Peru.

The field work thus covered the Pacific slope of South America from the Panama Canal to Puerto Montt in Chili.

Both in Panama (the Chagres) and Colombia (the Magdalena and Atrato) the work included streams emptying into the Caribbean, *i.e.*, the Atlantic. All of these are, however, west of the Cordillera of Bogota, at present an insuperable barrier to lowland fishes.

## ACKNOWLEDGMENTS

I must acknowledge the hearty cooperation of the authorities of Indiana University, and of the Republics of Colombia, Peru and Chili.

The expenses for my "Reconnaissance of Colombia" were met by the sale to the Carnegie Museum of Pittsburgh, Pa., of the first series of fishes and duplicates after a series had been set aside for Indiana University. Messrs. Hugh McK. Landon and Carl Fisher, both of Indianapolis, provided for the expenses of Messrs. Henn and Wilson in Colombia. Mr. Landon and Indiana University provided for Mr. Henn's expenses in Ecuador.

The Irwin Expedition, which collected in Lake Titicaca and on the Atlantic slope, as well as on the Pacific slope, was financed by a grant from the Bache Fund of the National Academy of Sciences, by two grants from the American Association for the Advancement of Science,

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[8] *Science*, N. S., L, pp. 100–102, Aug., 1919; *Indiana University Alumni Quarterly*, January, 1920, pp. 1–16.

[9] *Science*, N. S., LIII, pp. 377–379, 1921; *Indiana University Alumni Quarterly*, April, 1921.

by a gift from Mr. William Irwin of Columbus, Indiana, and by appropriations from the Universities of Indiana and Illinois.

The Centennial Expedition of Indiana University also had the cooperation of the Bache Fund of the National Academy of Sciences. Particular thanks are due to the various persons who cooperated with me in the field, Mr. Arthur Bierman, Mr. Arthur Henn, Mr. Charles Wilson, Dr. William Ray Allen, Mr. Nathan Pearson and Dr. Adele Eigenmann (Mrs. John Eiler).

## THE NATURE OF THE PACIFIC SLOPE BETWEEN THE PANAMA CANAL AND PUERTO MONTT

*Topography.*—In the region of the Panama Canal the continental divide is but 9 miles from the Pacific ocean. It is but 8 miles from the old city of Panama to the divide. East of this point it shifts toward the Atlantic. From opposite the Chepo about 79° W. to about 8° 15′ N. and 77° 15′ W. the crest averages about five miles from the Atlantic. At the latter point it turns southwest and from 7° N. to about 5° N. the crest of the coastal Cordilleras, which here forms the divide, varies from a few hundred feet to twenty miles from the Pacific. At 5° N. it suddenly shifts from the coastal to the western Cordilleras of Colombia to include the Rio San Juan basin in the Pacific slope. It runs along the crest of the western Cordilleras to the Rio Patia. This river has cut through the western Cordilleras and has captured some of the upper tributaries of the Rio Cauca of the Atlantic slope. South of the Patia, the Mira, Esmeraldas, Chimbo, Chanchan, Naranja, Romido, Tumbez, and Catamayo have also cut through the crest of the western Cordilleras translating the divide to the eastern Cordilleras. In Ecuador the continental divide runs along the eastern Cordilleras in the north, shifts from the eastern to the western (at 40′ S.) to the eastern again (just south of 2° S.) to the western once more (near 2° 30′) to the eastern once more (3° 20′). From northern Peru it follows the crest of the western Andes to Chili. In its widest part in Ecuador, near the equator, the slope is 160 miles from crest to ocean, in its narrowest part near 3° S., it is about 30 miles from the ocean. Here the Atlantic slope is one hundred times wider than the Pacific slope. In Peru the slope varies in width from about 50 miles to 150 miles. Between the northern border of Chili to Puerto Montt it varies from 50 to 200 miles in width. The average width between central Colombia and Puerto Montt in a length of over 3,000 miles is less than 100 miles. Between the Panama Canal and Puerto Montt the width varies from a few hundred feet to 200 miles.

The crest everywhere between central Colombia and Valdivia is at present an insurmountable barrier to the intermigration of all but the highest mountain fishes of the genera Orestias, Pygidium and Astroblepus. To the most of the species of even these genera the transmigration of the Andes has been and is impossible.

Strategic points in the continental divide are: (1) Culebra between the Chagres and the Pacific slope streams with a height of about 334 feet. (2) Cajal pass in eastern Panama, between the Tuyra of the Pacific and the Atrato of the Atlantic, with a height of about 400 feet. (3) The Istmina pass between the Atrato of the Atlantic and the San Juan of the Pacific with a height of about 300 feet. (4) The Patia, which has robbed the Cauca of the Atlantic slope. South of the Patia the continental divide is mostly over 9,000 and 10,000 feet, except inland from Piura where a saddle reaches an elevation of but about 7,000 feet. Just south of 40° S. in Chili the headwaters of the Calle Calle arise east of the main crest of the Andes. Near Puerto Montt a pass between the Petrohué Basin and the Nahuel Huapi Basin is but 3,000 feet high, and south of this point rivers of one side not infrequently have their origin on the other side of the main crest. The story of the shifting of the continental divide in Ecuador is repeated in southern Chili, but now at much lower altitudes.

*Moisture.*—The rainfall in different parts of the slope varies from nearly 400 inches per annum to nothing. In Panama, Colombia and northern Ecuador, the rainfall of the Pacific slope is excessive. In Piura, northern Peru, it rains once in many years. When at Piura I asked, "Where is the river?" I was told, "It has not come down yet; we expect it next Saturday." In the north the mountains cast rain shadows eastward. Southward the mountains cast rain shadows westward.

Southward of Guayaquil the rivers become more and more uncertain to northern Chili where only the mountain-fed Loa crosses the arid slope. South of the desert of Atacama rivers are again found occasionally. The first of them is the Rio Copiapo. Between La Serena and Vallenar, I was told that after a rain all the hills became covered with flowers. When I asked about the rainy season I was informed that it had rained once in those parts about eleven years before. In this arid region of Chili there are great valleys from crest to ocean but the rivers that made them are extinct and so naturally are the fishes that inhabited them.

South of Valparaiso valleys are also abundant and water becomes more and more abundant. The region between Concepcion with its Rio Bio Bio and Puerto Montt is supplied with numerous lakes and rivers. The rainfall in this region is again very great, but not so great as in Panama and Colombia. The region from Panama to the boundary of Chili lies in the tropics, the climate north of Guayaquil is tropical but south of Guayaquil temperate. The rivers of Chili between the Copiapo and Puerto Montt all lie in the south temperate region.

## THE NATURE, ORIGIN AND DISPERSAL OF THE FISHES

I have dealt with the details of the fishes of the Pacific slope of South America in a series of papers[10] published in various places.

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[10] 1. "Some Results from an Ichthyological Reconnaissance of Colombia, South America," *Indiana University Studies*, No. 16, Sept., 1912. (Issued December 23.)

There remains scarcely a doubt about the origin of any of the present genera of the entire Pacific slope. (Footnote 10, no. 14.)

2. "Some Results, etc.," Part II, *l. c.*, No. 18, March, 1913. (Issued in June.)
3. "New Fishes from Western Colombia, Ecuador and Peru" (in collaboration with Arthur Henn and Charles Wilson), *l. c.*, No. 19, January, 1914.
4. "Some Results from Studies of South American Fishes," *l. c.*, No. 20, March, 1914. (Issued in April.)
5. "On New Species of Fishes from the Rio Meta Basin of Eastern Colombia and on Albino or Blind Fishes from near Bogota," *l. c.*, No. 23, September, 1914.
6. "On New Species of Fishes from Colombia, Ecuador and Brazil" (in collaboration with Arthur Henn), *l. c.*, No. 24, September, 1914.
7. "The Gymnotidæ of Trans-Andean Colombia and Ecuador," *l. c.*, 25, September, 1914.
8. "South America West of the Maracaibo, Orinoco, Amazon, and Titicaca Basins and the Horizontal Distribution of its Fresh-water Fishes," *l. c.*, No. 46, pp. 1–19, map, September, 1920. (Issued January, 1921.)
9. "The Fishes of the Rivers Draining the Western Slope of the Cordillera Occidental of Colombia, Rios Atrato, San Juan, Dagua, and Patia," *l. c.*, No. 46, pp. 1–19, map, September, 1920. (Issued January, 1921.)
10. *A.* "The Fresh-water Fishes of Panama East of Longitude 80° W."
    *B.* "The Magdalena Basin and the Horizontal and Vertical Distribution of Its Fishes," *l. c.*, No. 47, pp. 1–34, maps, December, 1920. (Issued May, 1921.)
11. "The Fish Fauna of the Cordillera of Bogota," *Journ. Washington Acad. Sci.*, X, pp. 460–468, Oct., 1920.
12. "Eighteen New Species of Fishes from Northwestern South America," *Proc. Am. Philos. Soc.*, LVI, pp. 673–689, 1917.
13. "Description of Sixteen New Species of Pygidiidæ," *l. c.*, LVI, pp. 690–703, 1917.
14. "The Origin and Distribution of the Genera of the Fishes of South America West of the Maracaibo, Orinoco, Amazon and Titicaca Basins," *l. c.*, LX, pp. 1–6, 1921.
15. "The Nature and Origin of the Fishes of the Pacific Slope of Ecuador, Peru and Chili," *l. c.*, —, pp. —, 1921.
16. "The Cheirodontinæ, a Subfamily of Minute Characid Fishes of South America," *Mem. Carnegie Mus.*, VII, pp. 1–99, 36 text figures, plates I–XVII.
17. "*Pimelodella* and *Typhlobagrus*," *l. c.*, VII, pp. 229–258, plates XXIX-XXXV, 1917.
18. "The Pygidiidæ, a Family of South American Catfishes," *l. c.*, VII, pp. 259–398, 39 text figures, plates XXXVI–LVI, 1918.
19. "The Fishes of Western South America, Part I. The Fresh-Water Fishes of Northwestern South America, including Colombia, Panama, and the Pacific Slopes of Ecuador and Peru, together with an Appendix upon the Fishes of the Rio Meta in Colombia." *Mem.*

On the Pacific slope between Panama and southern Chili there are two main faunas. That of Chili belonging to the south temperate Patagonian fauna is flavored with but a suspicion of the tropics. It is poor in species, there being but 35 known species in all the rivers of Chili north of Puerto Montt.

The fishes of the rivers north of Lima pertain to the tropical fauna of the Amazon-Orinoco and Central America with but a few occasional north temperate surprises. Three hundred and eighty-five species have been taken in the rivers of Colombia west of the Cordillera of Bogota and on the Pacific slopes of Ecuador and Peru. This area is divisible into several distinct regions.

The highland fauna (above 7,000 feet) in part overlaps the different lowland faunas.

## The Fauna of Chili

The fauna of Chili, consisting of but thirty-odd species, is completely distinct from that north of Lima, Peru. A very large per cent. of it has immigrated from the ocean, a smaller part came from the north, another small part is autochthonous.

*Carnegie Mus.*, IX, 1922 (issued January, 1923), pp. 1–346, text figures, plates I–XXXVIII.

20. "On *Aparciodon*, a New Genus of Characid Fishes," *Ann. Carnegie Mus.*, X, pp. 71–76, plates XI–XII, 1916.
21. "New and Rare Fishes from South America," *l. c.*, X, pp. 77–86. Text figures 3, plates XIII–XVI, 1916.
22. "Description of Three New Species of Characid Fishes" (in collaboration with Arthur Henn), *l. c.*, X, pp. 87–90, plate XVII, 1916.
23. "On the Species of *Salminus*," *l. c.*, X, pp. 91–92, 1916.
24. "On Various South American Pœciliid Fishes," by Arthur Henn, *l. c.*, X, pp. 93–142, plates XVIII–XXI, 1916.
25. Report as Curator of Fishes in Carnegie Museum. Seventeenth Ann. Rept. of the Director, 1914, pp. 19–22.
26. "The Freshwater Fishes of Chili," nearly completed.
27. "Yellow Fever and Fishes," *Proceedings American Philosophical Society*, LXI, 1922, pp. 204–211.
28. "A Catalogue of the Freshwater Fishes of South America," *Proc. U. S. Nat. Mus.*, XIV, 1891, pp. 1–81. Aside from listing the species this paper discusses various phases of the distribution of genera, including those of the Pacific slope.

Part of the oceanic contribution came from the south and is common to Australia, New Zealand, Patagonia and Chili. The point of origin of this element of the fauna is in doubt, unless there was a habitable antarctic continent in which the Galaxiidæ, Aplochitonidæ and Lampreys developed and from which they moved north in all directions. In Chili this part of the fauna moved from its point of origin to different points north, some of the lampreys to Valparaiso, *Galaxias maculatus* and Aplochiton to Concepcion, other fishes apparently only to Valdivia, the northernmost point where the Lampreys, the Galaxiidæ, and the Aplochitonidæ are still at their best. The species are abundant in the streams having lakes in their headwaters.

The other oceanic contribution to the freshwater fauna came from the temperate sea. (*a*) The genus Cauque of the Atherinidæ is but little different from Austromenidia, at the present time abundant on the coast of Peru and Chili. Cauque occurs from La Serena southward (on both slopes). (*b*) The genus Basilichthys, also of the Atherinidæ, is of older standing, ranging in the rivers at least from Lima to Puerto Montt. In this range three species have become differentiated, one in Peru, one in Chili north of Santiago, and one south of Santiago. (*c*) The genus Percichthys, confined to Chili and Patagonia, from Punta Arenas as far north as there is suitable water (Rio Aconcagua) is a thoroughly freshwater genus belonging to the marine family of the Serranidæ. It is an ancient contribution from the sea. (*d*) The genus Percilia, also of the Serranidæ, probably has a similar history.

The contribution from the north consists of (*a*) Pygidium, a mountain catfish found in all the mountains of South America, (*b*) Hatcheria, a Patagonian modification of Pygidium, (*c*) Cheirodon, a minute characin ranging from Panama south (see no. 16, footnote 10), is the only contribution from the tropical fauna of South America. The presence of Cheirodon in Chili probably dates back to the time when Argentina was a suitable habitat for the genus as far south as the great lakes of Patagonia. It has retained its primitive structure in and near the Bio Bio basin. Less typical species have developed north and south of the Bio Bio region.

The third, the autochthonous element of the fauna, is the most ancient. It consists of but two species, *Nematogenys inermis* and *Diplomyste Chilensis.* (*a*) Diplomyste is found between Santiago and Buenos Aires on the north, and Valdivia on the south. It is autochthonous, one of the original Patagonians, a catfish in which the maxillary still carries teeth. (*b*) The last of the Chilian fishes is *Nematoyenys inermis,* confined to central Chili. It is the most primitive or generalized member of the Pygidiidæ, lacking some of the most characteristic features of the family, differing in fact so much that it might well be considered the type of a distinct family, the Nematogenyidæ. This genus is also autochthonous, the first, original "Chileno."

Chili is divisible into the following regions:

*a.* The "Austro-Chilian" extends north to Valdivia and is characterized by the abundance of Lampreys, Galaxias, and Aplochiton and the absence of Nematogenys. It is the region of the great lakes.

*b.* The "Intermediate" between Valdivia and Concepcion is characterized by the waning of the Galaxiidæ and Aplochitonidæ.

*c.* The "Chilian" from Concepcion to Santiago is characterized by Nematogenys, Diplomyste and the absence of Galaxiidæ and Aplochitonidæ.

*d.* The "Region of Relicts" north of Valparaiso. The rivers are small and many have gone dry altogether. Only Cauque, Basilichthys, Cheirodon and Pygidium have been taken north of the Rio Aconcagua; in Choapa only Basilichthys; in Vallenar only Cheirodon; in the Rio Camarones only Basilichthys. Basilichthys will probably be found in all the rivers of the dry region between Lima and Valparaiso that retain any encouragement for the continued existence of fishes.

The freshwater fishes of Chili and Patagonia are so limited in numbers and show such affinity with the marine fauna that I adhere to an opinion I expressed long ago. During the subsidence from which Chili and southern Patagonia are at present rising all the freshwater fishes except those adjusted to also live in the ocean were exterminated. There has not been time or opportunity since its reelevation to impart a new extensive purely freshwater fauna. In the north of Chili and Patagonia during the subsidence there were opportunities for the continued existence of Cheirodon, Pygidium, Nematogenys, Diplomyste and possibly Percichthys and Percilia.

The rate of elevation as measured on rocks outside of Coquimbo is about 25 feet in 200 years.

## THE FAUNA OF WESTERN ECUADOR AND PERU

(See Nos. 15 and 19, footnote 10)

The fauna of the Guayas in Ecuador was derived from the Amazonian fauna. It has less affinity to that of the Magdalena to the north of it than to that of the Amazon east of it. Its origin can best be explained on the assumption that at a time much earlier than the era of the continuity of the Magdalena fauna with that of the Orinoco there was a continuous fish fauna from the Pacific shores of Ecuador and northern Peru to the Atlantic shores. The development of the western Andes of Ecuador and northern Peru isolated the species living west of them from those living east of them. This isolation took place much earlier than the isolation of the Magdalena fauna by the Cordillera of Bogota. It took place before the development of the present species of Ecuador and before the development of many of the genera of the Guayas. Only one species of western Ecuador is also (possibly) found east of the Andes. Twenty-five per cent. of the genera of Ecuador are peculiar. South of Guayaquil, with the elevation of the Andes the genera and species have become exterminated one after another. The Peruvian rivers draining into the Pacific have at present torrential courses and great seasonal fluctuation which few species of the original fish-fauna have been able to withstand.

The Guayas fauna and the Chilian fauna touch in the Rio Rimac of central Peru where *Basilichthys semotilus* gives the first hint of the Chilian fish-fauna, *Brycona-mericus peruanus* and *Lebiasina bimaculata* are all that recall the Guayas. The present Guayas river is probably much younger than the fish-fauna it contains. In the early Quaternary it became the most favorable habitat for freshwater fishes on the Pacific slope and became the gathering place of the entire Pacific slope fauna of southern Ecuador and Peru. It is well separated from the north. Not more than four of its known species are also found north of it.

## THE FAUNA OF WESTERN COLOMBIA

(See Nos. 8, 9, 10, 11, 15 and 19, footnote 10)

The fishes of the Pacific slope of Colombia came in very large part from the Magdalena and Atrato basins. The Atrato fishes themselves came in large part from the Magdalena. While the Magdalena and Atrato are not Pacific slope streams, since they are west of an insuperable barrier and have contributed so much to the Pacific slope an examination at this point of the origin of the Magdalena fauna is warranted.

The nature of the Pacific slope and Magdalena fauna can best be explained by the following facts and assumptions: As in Ecuador the oldest of the mountain chains of Colombia is the Cordillera Occidental extending from the hills at Cartagena south to Cape Horn. The formation of this chain with the development of the rivers draining its slopes divided the primitive fauna of Colombia into a western and eastern as it did in Peru and Ecuador. The rivers of the western slope draining into the Pacific were short and the fauna was from the start more limited than the fauna of the much larger Atlantic slopes. In part the fishes of this early segregation were generically at least identical with those of western Ecuador and Peru. Others were peculiar.

As in Ecuador, the formation of this, the western, chain antedates the present species and many of the present genera. (See No. 9, footnote 10.)

The central Cordilleras of Colombia were the second of the Andean chains to develop. Their development formed the groove in which developed the upper Rio Cauca, the oldest of the larger rivers of western Colombia. If there has been a continuity of the fishes from that day to this, we should get an inkling of the old fauna in the twenty-nine species of fishes taken in the upper Cauca. The western Cordilleras, although in places but 6,000 feet high, have been an effective barrier to the migration of the present fishes of the upper Cauca to the rivers on the Pacific slope. (For details see Nos. 9 and 10, B, of the bibliography in footnote 10.)

The third of the mountain chains to develop are the Cordilleras of Perija and of Bogota. They segregated the Magdalena valley with its fishes from Lake Maracaibo and the Orinoco. The territory segregated by this uplift is much more extensive than that by former mountain formations. It resulted in the development of the Rio Magdalena.

The isolation of the Magdalena basin took place during the lifetime of most of the present dominant genera and during the life of many of the present species. Thirty-four of the species of the Magdalena have retained their specific characters since before the development of the Cordillera of Bogota divided their range. The stripes on the catfish, Pseudolatystoma, which is found on both slopes, are older than these mountains. (See No. 10, B, footnote 10.)

Before the elevation of the Cordilleras of Bogota began to form an effective barrier to the migration of freshwater fishes the area at present occupied by the Magdalena basin was inhabited, in common with the area to the east of the present Cordilleras of Bogota and

Perija, by a fish-fauna in many respects similar to the present fauna of eastern tropical South America at an elevation of five hundred to a thousand feet. The fishes belong to seventy odd genera. Of the latter the tarpon and eel were contributed by the north via the sea. Eight genera were contributed by Central America, five belong to the high Andes, over fifty are also found east of the Cordillera of Bogota, the rest are evident modifications of eastern genera.

As stated the Cordillera Occidental is the oldest mountain chain in Colombia. Its Pacific slope from the divide to the Atrato and San Juan in the north and the ocean in the south is narrow. Its development segregated a very limited part of the original fauna. The coastal Cordillera to the west of it is the youngest of the mountain chains in Colombia. Its development and denudation in late Tertiary (or Quaternary as Hettner suggests) caused the formation of the Atrato and San Juan rivers in the trough between the western and coastal Cordilleras. They gathered the waters of the small streams flowing originally direct from the Cordillera Occidental to the sea, the San Juan carrying the water of those south of Istmina into the Pacific, the Atrato carrying the waters of those north of Istmina into the Atlantic. The development of the large Atrato river provided a suitable environment for many of the fishes which had not found an environment in the small mountain torrents. Some of the fishes of the Magdalena migrating westward along the low coastal plain (via the Sinu?) and around the northern end of the western Cordilleras colonized the new environment provided by the Atrato. Some of the species that got into the Atrato went further, crossing the pass of Cajal into the Tuyra basin, others crossing the pass at Istmina into the San Juan basin. Some species that succeeded in crossing the divide at Cajal have not succeeded in crossing the pass at Istmina. Prochilodus and Leporinus have not succeeded in crossing either although there is favorable environment across both divides (see No. 9, footnote 10) and both genera are also found in Ecuador.

Over 60 per cent. of the known species of fishes of the Atrato came from the Magdalena or have diverged but slightly from Magdalena species.

Of forty-five species migrating westward from the Magdalena into the Atrato, twenty stopped in the Atrato, nine became but slightly modified, eleven got across the divide southward into the San Juan, three more got as far as the Dagua, and five more reached the Rio Patia. (See No. 9, footnote 10.)

The migration into the Atrato, Tuyra, Chepo and southward to the San Juan, Dagua, Patia took place much more recently than the isolation of the Magdalena from the Orinoco if the per cent. of identical species may be taken as a measure of time. The migration probably began before the Magdalena became entirely isolated from the east. About twenty per cent. of the Magdalena species still live east of the Cordilleras of Bogota. The per cent. of species of the western rivers still living in the Magdalena is much greater. Over sixty per cent. of the known Atrato species still live in the Magdalena basin or have representatives there. (There certainly are more.) Thirty-six per cent. of the San Juan species live in the Atrato. Sixty-five per cent. of the Patia (near the boundary of Ecuador) species live in the San Juan, Dagua, Atrato or Magdalena.

These per cents. of identical species in neighboring rivers give an inverse ratio of the length of time the rivers have been separated or of the difficulties for fishes to pass from one to the other.

## THE ORIGIN OF THE PANAMA FAUNA

The present fish-fauna of the Isthmus of Panama appears quite recent. The ancestors of the fishes of the Chagres river came in largest part from the south, in much smaller part from the north. The balance came from the ocean.

At least nineteen species have succeeded in crossing the Pass at Cajal, from the Atrato westward into the Tuyra. Others have crossed but have become modified in the Tuyra. Of these species which went from the Atrato to the Tuyra, eleven reached the Chepo and of these eleven, five recrossed the continental divide into the Chagres. (See No. 10A, footnote 10.) The fresh-water fishes of the Atrato have not been able to reach the Chagres by way of the sea. Thirty-eight per cent. of the Tuyra fishes live in the Atrato, thirty-one and five tenths per cent. of the Chepo fishes live also in the Tuyra; seventy-three per cent. of the fishes in the streams opposite the Chagres live also in the neighboring Chepo. Forty-two per cent. of the Chagres fishes live also in the Chepo or the Pacific slope streams opposite the Chagres. The similarities pointed out in this paragraph are for the most part the results of active migrations *since* the development of the Atrato.

The Chagres has received a large per cent. of its fishes from the Atrato via the Tuyra and Chepo. Only one of the Chagres fishes coming from the south (Atrato) has reached as far north as Costa Rica.

The Chagres has received a number of its species from the north. Of these a gar pike has come the farthest. It was recorded long ago but was not found in recent explorations. The common eel occasionally drifts into Panama. The genera Agonostoma, Jotarus and a number of Cichlids are Central American and find their farthest south in or near Panama.

Judging by the present fauna the present isthmus of Panama has not been used as a highway for the intermigration of northern and southern faunas. It is the present meeting place of a stream coming from the south and another coming from the north. (No. 10, footnote 10.)

## GENERAL ITEMS ON THE PACIFIC SLOPE OF ECUADOR AND WESTERN COLOMBIA

(See No. 19, footnote 10)

1. Certain of the generic types have undergone a very active evolution in this region, giving rise to many species; such are (1) Astyanax (14 species), (2) Bryconamericus (10 species), (3) Creagrutus (6 species), (4) Brycon (13 species), (5) Pimelodella (6 species), (6) Astroblepus (18 species), (7) Pygidium (22 species), (8) Chætostomus (6 species), (9) Loricaria (10 species), (10) Curimatus (8 species), (11) Hemibrycon (7 species), (12) Rœboides (7 species). The second and fourth of these genera have reached their optimum west of the Andes. All of these genera, except possibly 6, antedate the formation of the Andes.

2. Other genera are at present forming incipient new species. Such are Argopleura, Rœboides and Gephyrocharax.

3. The Glandulocaudinæ reach their highest development in western Colombia and in southeastern Brazil and Uruguay. (See No. 4, footnote 10.)

4. The highland fauna. (See Nos. 9, 10B, and 11, footnote 10.)

The highest altitudes are inhabited principally by species belonging to three genera: Pygidium, Astroblepus and Orestias. They are indifferently found both on the Atlantic and Pacific slopes. Astroblepus is found in all suitable places in the Andes from Panama to Lake Titicaca.[11] In Colombia it attains the highest altitude inhabited by fishes but descends in favorable places to 300 feet.

The species of Pygidium are found in all the mountains of South America; on the Pacific slope, all the way from Panama to Patagonia, from 14,000 feet to sea level.[12]

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[11] But one species has been found in the Titicaca basin.

[12] The Pygidiidæ have become of unsurpassed economic interest since the discovery by Dr. H. Hanson, of the Rockefeller Foundation, that one of the species of Pygidium (probably all of them) is of supreme importance

Orestias is confined to quiet water above 7,000 feet in Peru and northern Chili. It reaches its optimum in Lake Titicaca.

Pygidium and Astroblepus are mountain scalers, at their best in rapids. Orestias, on the contrary, belongs in quiet water. It could not have ascended to its present height by way of the present torrents. It went up with the Andes. One species of Orestias lives in Death Valley, between California and Nevada.

These three mountain genera to which should probably be added some of the species of Hemibrycon, a Characid and some of the species of Chætostomus, a mailed catfish, belong to an ecological group and obey laws of distribution quite different from those of the lower slopes of the Andes.

## THE GEOGRAPHICAL DISTRIBUTION OF THE ONYCOPHORA

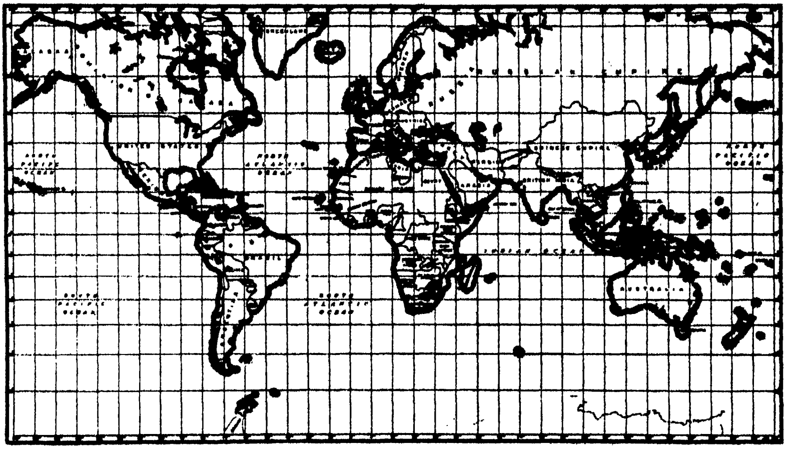
PROFESSOR CHARLES T. BRUES

BUSSEY INSTITUTION, HARVARD UNIVERSITY

THE Onycophora, familiarly known among zoologists as "Peripatus," now include about eighty species, grouped into more than a dozen genera that form two families. Although they have been thus subjected to the most minute classificatory dissection (Fig. 1) at the hands of the taxonomists, they remain to-day as isolated from any other group of animals as they appeared to be when Guilding, nearly a century ago, described *Peripatus juliformis* as an aberrant mollusc. That the group is now conceded to be more or less transitional between the Annelids and Arthropods is of no moment in the present connection, and we may be content with the statement, which can be made without reserve, that the Onycophora include a number of very closely related species, entirely different from any other animals, widely scattered throughout the tropics of both hemispheres.

in the eradication of yellow fever mosquito larvæ from the storage vessels for drinking water. See footnote 10, Nos. 18 and 27.

The oldest, and indeed the only known, fossil member of the group, *Aysheaia pedunculata* Walcott, has been found in the middle Cambrian rocks of North America; it does not seem to be remarkably unlike the living forms.

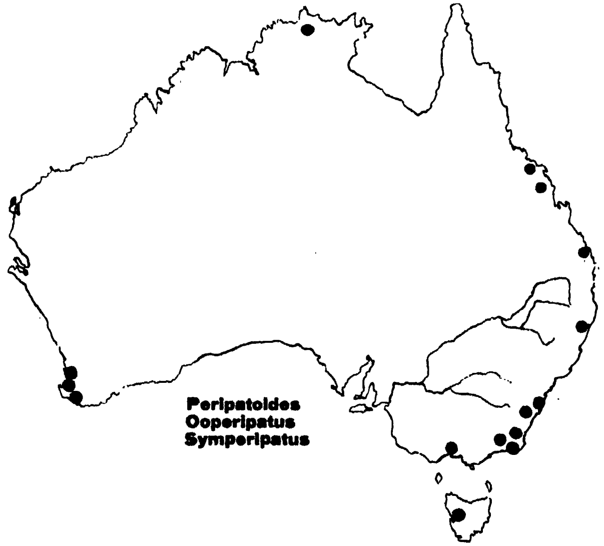


MAP I. World Distribution of Onycophora.

The Onycophora are of interest to the zoogeographer for several other reasons. They are soft-bodied, usually very delicate and sensitive creatures, of secretive habits, and restricted to very specialized habitats. They have thus, undoubtedly, found it very difficult to perform extensive migrations. Also, they are absolutely unfitted for transport by the elements, by rafts, or through the agency of other animals, due to their inability to survive for any length of time under adverse conditions. Similarly the eggs are delicate, and are never even laid by the females of many species, which have become viviparous and produce large living young. We see, therefore, that the present wide and discontinuous distribution of the group is of considerable interest. From Map I, it will be seen that the group occurs mainly in tropical America, South Africa, Australia, New Zealand, Malaya and Indo-China. As the species are often extremely local and erratic in their occurrence, it is unwise to lay great stress on the apparent absence of Onycophora from any area, but it is quite certain that the group is best represented in the tropical regions just mentioned, and that it is practically absent from the more temperate regions. Thus far no species are known from the Malagasy or Indian subregions and there is only one form recorded from equatorial Africa.

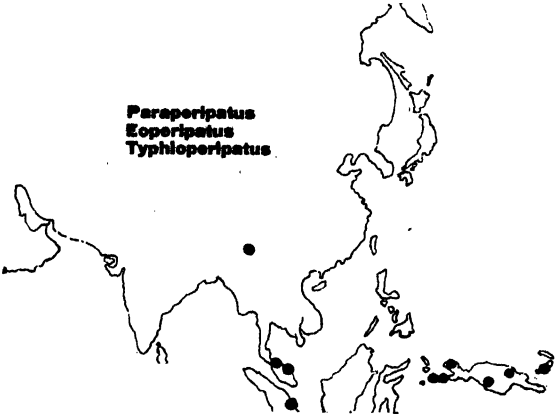
The most primitive family, the Peripatopsidæ, is restricted almost exclusively to the Old World, although one genus, Metaperipatus, occurs in Chile. The Peripatidæ occur in both hemispheres, the two genera of Eoperipatinæ in the Old World and the entire subfamily Peripatinæ in the New World, with the exception of the tropical African Mesoperipatus.

In Australia, including New Zealand and Tasmania (Map II), are three genera, Peripatoides, Ooperipatus and Symperipatus, sometimes included in a single genus and showing the close faunal relationship of Australia and New Zealand.



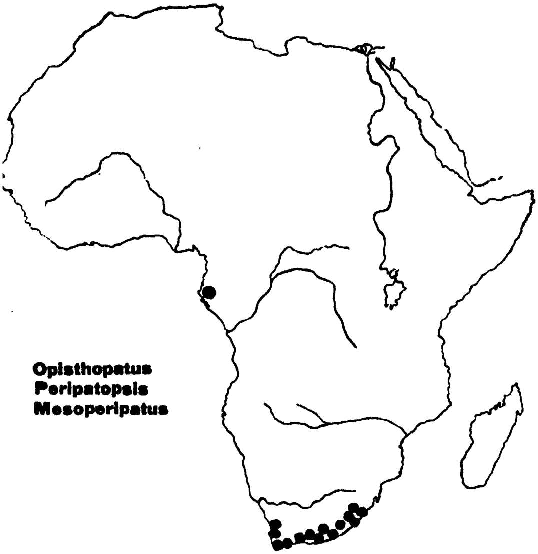
MAP II. Distribution of Onycophora in Australia.

In the region to the north (Map III) we find three genera, none of which occurs in Australia. Paraperipatus extends from New Britain through New Guinea into Ceram, but not further; to the west it is replaced by Eoperipatus known from Sumatra and the Malay peninsula. Typhloperipatus further to the north is a rather peculiar type, probably most closely related to Eoperipatus. Thus, in this much discussed Indo-Australian region we find "Wallace's line" separating the Peripatopsinæ and Eoperipatinæ.



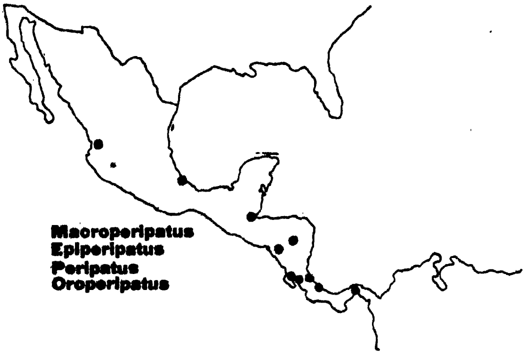
MAP III. Distribution of Onycophora in Asia and the East Indies.

In Africa (Map IV) we find three peculiar genera. In Cape Colony, Opisthopatus and Peripatopsis occur together and in apparently complete isolation from other genera. Likewise, Mesoperipatus is the only occupant of the equatorial belt. The single Opisthopatus is related to the Australian Peripatoides and also to a South American genus Metaperipatus, indicating migration probably from Australia to South Africa and thence to America, or possibly first to South America. On the other hand, the second South African genus, Peripatopsis, shows a close relationship to the Ceramese and Papuan Paraperipatus, indicating that there has at some time been an opportunity for migration between these two regions. The African Mesoperipatus is the only member of the Peripatinæ known from the Old World. It has been reported only from the French Congo. This genus combines certain antomical characters of two neotropical types in addition to some peculiarities of its own. From this we may surmise that it has been derived from some ancient neotropical immigrant that reached Africa from some portion of the South American continent.



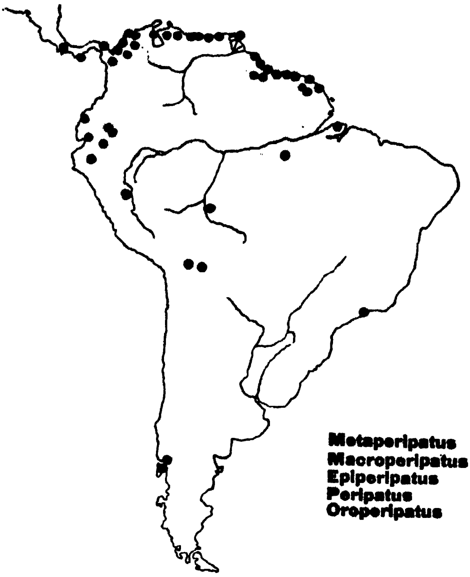
MAP IV. Distribution of Onycophora in Africa.

The Onycophora are, as we have already indicated, well represented in tropical America, ranging from well up in Mexico at Tepic to south-central Chile (Maps V,



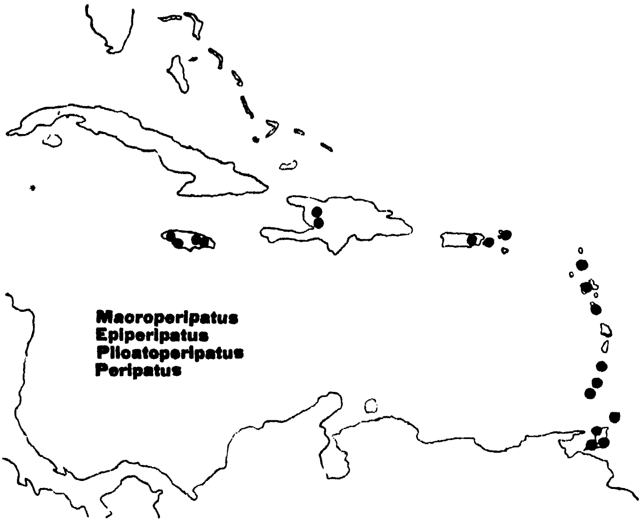
MAP V. Distribution of Onycophora in Central America.

VI, VII). Omitting a single discordant element, represented by the Chilian Metaperipatus, all are quite similar and form the subfamily Peripatinæ, typical of the New World and restricted to it, except for the African Mesoperipatus, already mentioned. Metaperipatus is referable to the Peripatoidinæ and finds its closest affinities among the African and Australian genera of that group, furnishing another example of faunal relationship between these three areas.



MAP VI. Distribution of Onycophora in South America.

The remaining truly American Peripatinæ fall into five types, all of which I have indicated for convenience on the taxonomic chart (Fig. 1) as genera. They are of unequal value and none are so closely set off as the genera we have previously discussed. More than half of the known species fall into this series, so that considering their similarity and the difficulty in distinguishing many of the species, it is evident that America is at present the seat of a quite active evolution and differentiation of onycophorous genera, species and subspecies. In the Andean Cordilleras and along the Pacific coast are a number of species of Oroperipatus. Some ascend to quite high altitudes in Ecuador and



MAP VII. Distribution of Onycophora in West Indies.

Bolivia, while others occur at sea-level, thus showing a very considerable tolerance to the variable climatic factors of temperature and humidity. Epiperipatus occupies the low-lying, moist, forested areas of the Spanish Main from whence it extends up the Amazon valley, northwards into Guatemala and along the Lesser Antilles to Grenada. Northward from Grenada its place is taken by Peripatus (*sensu stricto*) which has been found in the higher, humid parts of every one of the islands of any size from Carricau to Jamaica, except Martinique and St. Lucia. Strangely enough, however, Cuba has so far yielded no examples and is apparently lacking in Onycophora. Peripatus (*sensu stricto*) occurs also along the Caribbean coast from Costa Rica to Venezuela, thus more or less encircling the Caribbean. As all the species of this group are viviparous and perhaps the most delicate of all Onycophora, they must undoubtedly have reached all the islands over land bridges, or if we object to this term, *via terra firma*. Their absence from the adjoining islands of Martinique and St. Lucia in the middle of the series may be apparent only. If real, it may probably be traced to extinction through volcanic activity, since as we have already seen, the Antillean species are very delicately adjusted with reference to moisture. One other point of interest in connection with the Lesser Antilles is the occurrence of a continental type, Macroperipatus, on Trinidad, beyond which it does not go, although the continental affinities of Tobago and Grenada just to the north are vouchsafed by the extension of Epiperipatus into these islands.

- **Peripatopsidae**
  - **Peripatoidinae**
    - **Peripatoides**
    - **Ooperipatus**
    - **Symperipatus**
    - **Opisthopatus**
    - **Metaperipatus**
  - **Peripatopsinae**
    - **Peripatopsis**
    - **Paraperipatus**
- **Peripatidae**
  - **Eoperipatinae**
    - **Eoperipatus**
    - **Typhloperipatus**
  - **Peripatinae**
    - **Mesoperipatus**
    - **Macroperipatus**
    - **Epiperipatus**
    - **Plicatoperipatus**
    - **Peripatus**
    - **Oroperipatus**

FIG. 1. Taxonomic grouping of the genera of Onycophora.

Finally we must not fail to mention a striking type, Plicatoperipatus, represented by a single species, peculiar to Jamaica, lying geographically at the extreme western end of the series of Antillean stations so far reported for Onycophora.

# THE GEOGRAPHICAL DISTRIBUTION OF INSECTS AND THE AGE AND AREA HYPOTHESIS OF DR. J. C. WILLIS

DR. PHILIP P. CALVERT

UNIVERSITY OF PENNSYLVANIA, PHILADELPHIA

THE English botanist, Dr. John Christopher Willis, some time Director of the Botanical Gardens at Rio de Janeiro, has for the last twenty years devoted much attention to the study of geographical distribution and dispersal of plants. His conclusions have appeared in a number of papers from 1906 on and they have now been gathered up into a volume entitled, "Age and Area, a Study in Geographical Distribution and Origin of Species" (Cambridge, University Press, 1922). The main idea running through this book is what he terms the "rule of Age and Area," stated in his own words as follows:

> The area occupied at any given time, in any given country, by any group of allied species at least ten in number, depends chiefly, so long as conditions remain reasonably constant, upon the ages of the species of that group in that country, but may be enormously modified by the presence of barriers such as seas, rivers, mountains, changes of climate from one region to the next, or other ecological boundaries, and the like, also by the action of man and by other causes (p. 63).

In another place in the same volume, it is stated thus:

> As already several times explained, the general meaning of Age and Area is simply that on averages and in the long run species and genera spread at a more or less uniform rate, interfered with by barriers physical or ecological. On the older view it was imagined that distribution was so rapid that all forms had already reached their limits and that many were in process of contracting their area of dispersal (p. 189, footnote).

In their early stages of growth, Dr. Willis's views were largely derived from a study of the flora of the Island of Ceylon. Some of the species of this island are confined to it, others are found in Ceylon and in the Peninsula of India but not farther, still others, called for convenience sake the "wides," are found in Ceylon, Peninsular India and in more distant countries. This last class, or "wides," he believes to be the oldest of the three, the second class to be next in age and the first, or species endemic to Ceylon, to be the youngest. Just because they are the youngest they are confined to Ceylon, or even to limited parts of the island, since they have not had time to spread farther. He goes on to explain:

> It is clear, of course, that age in itself can effect nothing, but it allows time for the various factors that are active in distribution to produce their effects. . . . Dispersal therefore becomes a measure of age, except in so far as barriers, physical or ecological, interfere. Distribution is very slow, and probably the vast majority of species have not yet reached the limits that they might reach, if sufficient time were allowed (p. 61).

Some of the conclusions which Dr. Willis reaches with respect to the distribution of living things, both plants and animals, are as follows:

Those species which are most widely distributed in a country are those which have the widest distribution outside thereof while the local or endemic species show the smallest areas of distribution (p. 8).

Endemic species in all regions of the world belong in greater proportion not to the small and local genera but to the large and widespread (p. 165).

The species of endemic genera show less dispersal in a country than the endemic species of non-endemic genera (p. 166).

Distribution of genera within families or of species within genera, whether endemic or "wide," in any given area form "hollow curves," or curves with the mode at one end. This mode corresponds to the maximum number of genera within some larger taxonomic unit, but each genus containing only a single species (monotypic genera). From the mode the curve falls steeply and then gently declines to the minimum number of genera, but each (or the single) genus has the maximum number of species. The mode of maximum number of genera corresponds also to the smallest area of distribution, while the other end of the curve corresponds to the largest area (p. 166, combination of nos. 6, 7 and 10).

Curves of this nature have been drawn by Dr. Willis for many groups of plants, of various floras, and for some groups of animals and samples are given on p. 237. The numbers for such a curve of the Tenebrionid beetles, taken from Gebien, in the *Catalogus Coleopterorum* of 1910–11, are given as 489 genera of 1 species each, 154 of 2 species each, 103 of 3, 73 of 4, 40/5, 48/6, 32/7, 32/8, 24/9, 10/10 and so on (p. 203).

"Within any circle of affinity, the larger genera will be the older, and when taken in groups of ten allied genera will be older in rough proportion to their numbers of species" (p. 107). While this book says little of the actual ages of the taxonomic units discussed, we are told that the ages are to be "deduced from phyletic, morphological and geological considerations" (p. 108).

The main object of the present paper is to consider the possible application of these conclusions to certain insects.

At the outset, it must be premised that the data on the distribution of insects are not as definite or complete as in the case of plants. This condition is due to insects' powers of locomotion, both as favoring their wider distribution as well as eluding the collector; to the smallness of size of many of the species; and to their concealment on, under or within a great variety of objects.

The dragonfly,[1] or Odonate, fauna of New Jersey embraces 123 species of 44 genera.[2] The number of species in these genera correspond fairly well to Dr. Willis's hollow curves, when their fewness is considered, and are as follows: 25 genera of 1 species each, 6 of 2, 2/3, 5/4, 2/6, 1/9, 1/10, 1/12, 1/17.

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[1] The name of *dragonflies* had long been employed in English-speaking countries to designate the entire order of Odonata before its limitation to one of the two suborders (Anisoptera) appeared in publications from Cornell University. It has always seemed to me preferable to continue its older and wider use.

[2] J. B. Smith, *Ann. Rept.*, N. J. State Museum for 1909, pp. 73–82; H. B. Weiss in *Entom. News*, March, 1915, and Jan., 1916; A. S. Nicolay, *op. cit.*, Dec., 1919, and unpublished notes of the present writer.

A division of the State into six more or less well-defined physiographic regions has been mapped.[3] On listing the species found in each of these regions, only five species (*Lestes rectangularis, Ischnura posita, Anax junius, Libellula pulchella, Sympetrum rubicundulum*) are found in all six. Eleven others,[4] however, are known from five of these regions and it is highly probable that they also occur in all six. All of these sixteen are widespread in North America east of the Rocky Mountains; one of them (*Anax junius*) occurs also in the West Indies, on the Pacific coast of North America, in the Hawaiian Islands and has been reported from Tahiti, Kamchatka and China; another (*Anomalagrion hastatum*) reaches southward to Costa Rica and Venezuela, Cuba, Hayti and the Galapagos Islands; three (*Plathemis lydia, Erythemis simplicicollis* and *Pachydiplax longipennis*) reach British Columbia; the *Erythemis* and the *Pachydiplax* are known from Mexico, the *Erythemis* in the West Indies, the *Pachydiplax* in the Bermudas. On the other hand, certain species which thus far have been found only in one region in New Jersey are almost or equally as widespread (*Lestes congener* and *uncatus, Argia translata, Enallagma ebrium* and *hageni, Ophiogomphus rupinsulensis, Progomphus obscurus,* etc.). In at least some of these cases, we may suspect that the data from New Jersey are incomplete. The important fact for our present purpose is that these sixteen widespread species, even within their respective families, are on morphological grounds of very different ages, *Libellula* for example representing a more primitive condition than *Erythemis, Sympetrum* or *Pachydiplax.*

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[3] Smith, *op. cit.*

[4] *Calopt. maculata, Enal. civile, Isch. verticalis, Anomalagr. hastatum, Gomphus exilis, Epiæschna heros, Libellula cyanea, L. semifasciata, Plathemis lydia, Erythemis simplicicollis, Pachydiplax longipennis.*

The only species which from our present knowledge, or ignorance, may be looked upon as endemic in New Jersey are *Enallagma recurvatum* and *Somatochlora provocans*,[5] both of which belong to genera found throughout much of the holarctic region. No genera are endemic.

That group of damselflies which de Selys included in the legion Agrion consists in New Jersey of 33 species belonging to the 8 genera, *Argia* (6 species), *Chromagrion* (1), *Nehalennia* (2), *Amphiagrion* (1), *Enallagma* (17), *Telagrion* (1), *Ischnura* (4) and *Anomalagrion* (1). We have no sufficient geological or paleontological data to determine the relative ages of these genera, but, as far as one may deduce them from morphological considerations, *Argia* would seem to have the best claims to be the most primitive (earlier) and *Anomalagrion* the most specialized (later) genus.

Considering the distribution of these eight genera throughout the world, we find that *Argia* has more than 70 species but is confined to the Americas, *Chromagrion* has but one species extending from Maine and Quebec to New Jersey and Indiana; *Nehalennia* has 7 or 8 species from China, Europe, the United States (3 or 4) and Brazil; *Amphiagrion* has 2 species from the United States and Lake Titicaca; *Enallagma* 50 or more species, chiefly in North America, but some in Europe and northern Asia, and some of doubtful affinity in Africa and southern Asia; the six species of *Telagrion* are, with the exception of the one species from the Atlantic seaboard of the United States, from Trinidad and Brazil; the more than 30 species ascribed to *Ischnura* are from all parts of the world; the distribution of the only species of *Anomalagrion* has already been stated.

Looking only at *the total numbers of species in the world* in these genera, *Argia* would, by one of Dr.

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[5] I can not find the data on which Pennsylvania is included in the range of *S. provocans* in Muttkowski's Catalogue of the Odonata of North America, page 132.

Willis's rules, qualify as the oldest, *Ischnura* as much younger and *Enallagma* occupy a position between the other two. The area occupied by *Ischnura,* however, is more extensive than that of either of the other two. In New Jersey, the numbers of species give a different order, viz.: *Enallagma* 17, *Argia* 6, *Ischnura* 4.

It would therefore appear that the areas of distribution of the genera and of the species and the numbers of the species within each genus of the Odonata of New Jersey afford very few hints as to the relative ages of the taxonomic units.

The Odonata are animals with great inherent powers of dispersal and in the United States even the most endemic species occupy relatively extended areas. What has been learned of various species during the last twenty-five years[6] should impose great caution in asserting that any species of Odonata is of very limited distribution.

For these reasons the Odonata make a poor showing when tested by Dr. Willis's hypothesis of *Age and Area* and we turn to another group of Insects in which powerful and sustained flight is not a marked characteristic.

We owe to my colleagues in the Academy of Natural Sciences of Philadelphia, Messrs. J. A. G. Rehn and Morgan Hebard, an interesting and excellent paper on the Dermaptera and Orthoptera of the Coastal Plain and Piedmont Region of the southeastern United States.[7] In it the distribution of the species is tabulated in very convenient form, so that it is possible to take from it with great ease figures which may be compared with Dr. Willis's conclusions. The scope of the paper is Virginia, North and South Carolina, Georgia and northern Florida; 251 species and geographic races belonging to 100 genera comprise the Dermapterous and Orthopterous fauna of these states. They are tabulated both by physiographic regions and life zones and between these two categories a very considerable degree of correspondence exists.

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[6] For example, up to 1899, *Calopteryx angustipennis* was known only from a single male collected in Georgia by Abbott in the eighteenth century, one female from Kentucky and two other females of unknown provenance. In that year it was found in abundance in western Pennsylvania by Mr. E. B. Williamson.

[7] *Proceedings,* Acad. Nat. Sci., Phila., Vol. 68, pp. 87-314, 3 pls. 1916.

Six species, three of them probably introduced by man, two of them cockroaches, are generally distributed from the Boreal to the Sabalian (or lower division of the Austroriparian) life zone. As the data for the Boreal zone in general are stated by the authors to be very scanty, the following remarks leave it out of consideration.

Seventy-one species are tabulated as confined to one life zone in the southeastern states, but only 32 of these 71 are confined to these states or the immediately adjoining states. The remaining 39 are of wide distribution. The 32 species may be styled "possibly endemic" for convenience here; none of them belong to monotypic genera; 20 of the 32 are of the family Acrididæ (short-horned grasshoppers) and of these 20, 11 belong to the large genus *Melanoplus* (which contains over 200 species but is limited to North America) and the generic areas of the other 9 species are fairly wide although the numbers of species in their respective genera are not nearly so great. We may add that the distribution of the 242 species of the families Acrididæ, Tettigoniidæ and Gryllidæ of the southeastern states into genera forms a hollow curve, incomplete, but approximating those of Dr. Willis. Thus far these Orthoptera agree with Dr. Willis's conclusions quoted but when we attempt to determine the age of genera and species from the present areas of distribution in the southeastern states we seem to be left in the dark. The genera whose species singly or collectively occupy all five of the life zones or four of them (excluding the Boreal on account of the meagerness of the data therefor), and which have the largest numbers of species, should be the oldest, if Dr. Willis's conclusions are sound. There are 11 genera of the Acrididæ which fulfil this condition as to area and their respective numbers of species in the southeastern states range from 1 (*Dissosteira*) to 34 (*Melanoplus*) with an average of 5.6 species per genus. We doubt whether any student of the Orthoptera will regard *Melanoplus* as the oldest genus of Acrididæ in these states. Mr. Rehn tells me that he considers *Podisma* a much older grasshopper. Thirty-one species from North America, Europe and (mostly northern) Asia were catalogued by Kirby in 1910, a greater area, therefore, than that of *Melanoplus*. *Podisma glacialis variegata* is listed by Rehn and Hebard (page 96) as from "High Appalachian summits only." Although paleontological data on Acrididæ are scanty, it is of some interest to note that one *Dissosteira* and one *Hippiscus* are recognized in the European Miocene.[8]

On the principles of *Age and Area* the oldest genera of Tettigoniidæ (long-horned grasshoppers, katydids) in the southeastern states should be *Orchelimum* and *Conocephalus* and the oldest of the Gryllidæ (crickets) *Nemobius*. One species of *Orchelimum* has been listed from the Miocene of Florissant, four of "(*Nemobius*)" from the European Oligocene and two of *Gryllus* (which Mr. Rehn inclines to regard as an old cricket) from the Oligocene and Miocene of Europe.[8] Can the claims of these four genera to high antiquity be accepted from the standpoint of morphology?

The Carabidæ, or Ground Beetles, have still more limited powers of flight than the Orthoptera; 356 species have been listed from New Jersey.[9] The 72 genera, in which they are placed, again form approximately one of Dr. Willis's hollow curves. Species found in five or in all six of the physiographic regions of the State previously mentioned belong to every one of the categories of genera from that with one species to that with 36 species, but the *proportion* of genera with these *"wide" species within the State* steadily increases from the genera with one species each onward,[10] as one might expect. Between the extent of distribution outside of New Jersey of a "wide" New Jersey species belonging to a genus with a few species (*e.g., Scarites*) and that of a "wide" New Jersey species of a many-specied genus (*e.g., Calosoma, Amara*) there is often little to choose. Some species thus far recorded from only a single locality in New Jersey have a wide distribution outside of the State (*e.g., Lebia marginicollis, Chlænius prasinus, Harpalus convivus*); such cases are probably due to incomplete data. There appear to be no species endemic in New Jersey. The genus with the largest number of species in the State is *Platynus* with 36, followed by *Bembidium* (*Bembidion*) with 23, *Pterostichus* and *Amara* each with 21. The numbers of species in America north of Mexico for these genera are *Platynus* 87, *Bembidion* 369, *Pterostichus* 81 (now under two genera), *Amara* 179 (now under 6 genera).[11] American Tertiary fossils have been referred to 19 species of *Platynus* (1 of them Eocene), 12 species of *Bembidion* (1 of them Eocene), 10 species of *Pterostichus* (Miocene and later) and 6 species of *Amara* (Miocene). European fossils referred to these genera are of no greater age, but one European species of *Carabus* is of the Eocene and a *Galerita* is known from the Eocene of Green River, Wyoming.[12] Dr. Willis would doubtless conclude that *Bembidion* is an excellent illustration of Age and Area. Mr. Leng has kindly written me, how-

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[8] Handlirsch, "Die Fossile Insekten," pages 687, 688, 683, 685, 686.

[9] Smith, *l. c.;* Weiss, *l. c.*, and *Ent. News*, April, 1916, May, 1917, and Oct., 1918; Nicolay, *l. c.*

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[10] The actual figures are 26 genera with 1 species each (6), 16 with 2 (7), 9/3 (5), 2/4 (1), 1/5 (1), 2/6 (1), 3/7 (3), 3/9 (3), 1/13 (1), 1/15 (1), 1/16 (1), 2/17 (2), 1/19 (1), 2/21 (2), 1/23 (1), 1/36 (1). The numbers in parentheses are those of the numbers of genera in each category having one or more species in five or all six physiographic regions of New Jersey. The generic groupings employed in Leng's Catalogue of the Coleoptera of America, North of Mexico, will make some difference in the figures.

[11] Leng's Catalogue cited.

[12] Wickham in Leng's Catalogue; Handlirsch, "Die Fossile Insekten," p. 705.

ever, "the very numerous species of *Bembidion* and allied genera composing the tribe Bembidiini characterized by the stubby, subulate, last palpal joint and other highly derivative characters seem to me very recent. On the other hand, the eight-segmented abdomen and the comparatively soft pubescent elytra of *Brachinus* seem to me like a survival of primitive characters."[13] *Brachinus* has 13 species in New Jersey, 27 in America north of Mexico and to it have been referred two North American and one European fossil species, all of Miocene age. If *Brachinus* be entitled to the veneration which Mr. Leng suggests, its paleontological deficiencies must be shouldered by our long-suffering friend, "The Imperfection of the Geological Record."

It is very true that the areas inhabited by the insects thus far discussed are not sharply defined, as they are more or less arbitrarily designated parts of a great continent. Dr. Willis's results were largely obtained from a study of the floras of islands, especially Ceylon, New Zealand, Great Britain, whose physiographic limits are consequently clear and distinct, but he expressly extends his conclusions to just such continental areas as those which we have considered here for insects, *e.g.*, the flora of Cambridgeshire, the birds of British India, the endemics of Brazil (pp. 236, 237).

To turn briefly to an island fauna, there are 68 species of Odonata recorded from Cuba and the nearby Isle of Pines.[14] They are assigned to 37 genera and exhibit a more perfect hollow curve than any of the three previous cases: 23/1, 6/2, 3/3, 2/4, 2/5, 1/6. Five species are believed to be strictly endemic in these two islands; one of the five is of the monotypic and endemic genus *Microneura* which has morphological claims to being specialized, hence of recent origin; two are of the genus

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[13] See also the Introduction to his Catalogue, page 29.

[14] See *Trans. Amer. Ent. Soc.*, XLV, pp. 335–396, 1919; *Biol. Cent.-Amer. Neur.*, Introduction, Table B, 1908; also Kolbe, *Arch. f. Naturgesch.*, Jahrg. 1888, Bd. I, H. 2, pp. 153–178, taf. XIII; Kahl, *Ann. Carnegie Mus.*, X, pp. 519–526, 1916.

*Neoneura*, which is probably less specialized as a whole than *Microneura* and contains 17 species ranging from Cuba and Texas to southern Brazil; the remaining two are *Enallagma truncatum* and *Progomphus integer*, genera of still wider range, neither of which is apparently very old nor very young. Ten other species[15] are confined to the greater Antilles; two of the ten are of genera not known to extend beyond this group of islands, viz.: *Hypolestes* (with one other species in Jamaica) and the monotypic *Scapanea;* six species are of widespread tropical American genera and the remaining two are of the cosmopolitan *Lestes*, having more than 75 living species. I am disposed to regard *Lestes* as ancient, but this opinion is not universally shared by students of the Odonata, and I should look on *Hypolestes* as still older. *Protoneura* is decidedly specialized by reduction, going beyond *Microneura*. *Telebasis* and *Erythrodiplax* are not pronouncedly antique or modern; *Perithemis* may be older. *Dythemis, Scapanea* and *Macrothemis* seem of recent origin—all this, of course, on purely morphological evidence.

Incidentally, an unexplained riddle in geographical distribution is why the large and apparently strong *Scapanea frontalis*, with the favoring trade wind, has not been found on the mainland to the west. Considering it and the feeble flight of *Anomalagrion hastatum*, whose wide range has been given earlier in this paper, we are impressed with the fact that power of flight alone does not determine the dispersal of dragonflies. *Scapanea* and *Anomalagrion* are both monotypic, both have near allies, both appear to be specialized, and hence relatively recent forms, within their own families, yet their respective areas differ greatly in extent, that of the tiny *Anomalagrion* including all of the territory in which *Scapanea* is found and very much more beyond.

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[15] *Lestes spumaria, L. scalaris, Hypolestes trinitatis, Protoneura capillaris, Telebasis vulnerata, Dythemis rufinervis, Scapanea frontalis, Macrothemis celeno, Erythrodiplax connata justiniana, Perithemis domitia domitia.*

Here in the Odonate fauna of Cuba, as in the examples previously given, I fail to find the key to the origin and evolution of species with the ease which Dr. Willis's commendation of Age and Area would lead me to expect and which I would welcome if the key but turned in the lock.

# THE DISTRIBUTION AND DERIVATION OF SOME NEW ENGLAND ECHINODERMS

DR. HUBERT LYMAN CLARK

Museum of Comparative Zoology

Although naturalists no longer question the belief that existing species are the descendants of earlier forms by some process of evolution, there is still a considerable body of popular dissent encouraged by ignorant, even though often well-meaning, leaders. It is therefore worth while to marshal all the facts that can be of service in demonstrating the truth, and this is my excuse for offering the following statement concerning the distribution of New England echinoderms. The facts are not offered as new nor are the conclusions surprising, but both may be of use in confirming our faith in organic evolution.

Of the 46 species of echinoderms known to occur on the New England coast, there are at least half a dozen (all holothurians) concerning which our knowledge is too incomplete to permit us to discuss their distribution, but of the remaining 40, we know enough to warrant the attempt to interpret their derivation in the light of their distribution. Of these 40, 32 are certainly allied to a northern fauna, while 8 seem to represent a southern group. Naturally enough, the northern forms reach the southern limit of their distribution on the New England coast; few of them occur south of Nantucket and then only in deep, cold water. And of course, the southern forms find their northern limit along the southern coasts of Massachusetts, only one or two occurring north of Cape Cod.

Perhaps the best example of the northern group is the common green sea-urchin of the Maine coast (*Strongylocentrotus dröbachiensis*) whose scientific name has so long served as a stumbling-block to the zoological beginner and an awful example of much that a technical name should not be! The distribution of this urchin is very extensive; it is practically circumpolar in the Arctic regions though there are areas, both on the American and Siberian coasts, where it has not yet been taken; on the eastern side of the Atlantic, it comes as far south as Denmark and Scotland regularly, being common on those coasts, and it has been recorded from Holland, from the English Channel and even from near Madeira, in 100 fms.; in the western Atlantic, it ranges southward at least to Nantucket and in deep water to New Jersey and has been reported from as far south as Florida; in the eastern Pacific, it occurs regularly as far south as Oregon and specimens in the Museum of Comparative Zoology are labelled, on excellent authority, as from Hilo, Hawaii;[1] finally, in the western Pacific, it ranges to lat. 38° N. on the eastern coast of Japan and to lat. 37° N. in the Sea of Japan. Its bathymetrical range is from tide-pools to a depth of 1600 m. while its temperature range is even more remarkable, as it has been taken in water where the temperature was only 29.8° F., and yet it occurs abundantly in water of 50°–56°. It is not strange that having so wide a range, in every sense, the green sea-urchin is very variable and shows remarkable diversity in form and color and even in certain structural details, which may be associated with peculiarities of habitat. And yet neither on the European or American coasts is there any constancy in these peculiarities and no varieties are recognized nor is any closely related species of the genus known. In the Pacific, on the other hand, we find a very different state of affairs. The genus is almost certainly of North Pacific origin and there seems no reason to doubt that *dröbachiensis* has spread both eastward and westward from the northern end of Behring Strait. On the coasts of Japan are at least four other members of the genus and two or possibly three more occur on the Pacific coast of North America. But the specific limits of some of these species are ill-defined and their separation from *dröbachiensis* is not always clear cut. In the north, among the Aleutian and Kurile Islands, all the Strongylocentroti are either *dröbachiensis* or so very closely allied that their distinctness is open to grave doubt. But the farther south one goes in either the western or eastern Pacific, the more evident is the segregation of distinct forms. Off the coast of Oregon and California, in moderately deep (85–850 m.) and moderately warm (56.5°–41°) water, there is a well-marked species, *S. fragilis* Jackson, the distinctive features of which might be produced by carrying to an extreme some of the characters shown by deep-water specimens of *dröbachiensis*. Thus the spines are relatively long, slender and brittle, the test is thin and fragile and the color is more or less red orange, though the test is often purple. No one who compares specimens of *fragilis* with a good series of *dröbachiensis* from the coast north of Oregon can have any doubt of a genetic connection. There may be room for difference of opinion as to whether the remarkable variability of *dröbachiensis* is the cause or the effect of its extraordinary geographical, bathymetrical and thermal range, but there is no doubt of their correlation and there is therefore unusual material and opportunity for the formation of new species.

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[1] The specimens reported from near Madeira and from Hilo are difficult to account for, but in view of the remarkable temperature-range of *dröbachiensis* it is not absurd to suppose that they may have been carried to those warm spots on the foul bottoms of vessels which had been for some time previously in Scottish or in Alaskan ports. It seems probable that the specimens found at Hilo were dead when picked up along shore, the warm harbor water proving fatal after their long journey from colder seas.

Many other boreal echinoderms show a distribution and a variability more or less similar to that of the green sea-urchin. Lack of space forbids taking these cases up in detail but a few of them may be mentioned. The so-called sun-star, one of the characteristic sea-stars of the Maine coast, *Crossaster papposus,* has almost precisely the same range as *Strongylocentrotus dröbachiensis,* though it occurs normally farther south and west on the British coasts. Crossaster too like Strongylocentrotus is a north Pacific genus with only the single species in the north Atlantic. Our American authority on sea-stars, Dr. Walter K. Fisher (1911, Bull. 76, U. S. Nat. Mus., p. 326), says of *C. papposus:* "The North Pacific specimens are also variable, so much so in fact, that the extremes are very unlike. The species tends to form small varieties differing with locality and also with depth. . . . The forms listed herewith as . . . *papposus* may in reality be small species but it has not been possible to separate them on account of intergrades. With the exception of the Japanese specimens, which are believed to constitute a distinct species, all the North Pacific varieties have been called . . . *papposus.*" This is strikingly similar to conditions in Strongylocentrotus.

Among the brittle-stars, there is a case of distribution and differentiation into varieties, subspecies and species, of the same sort as the two first given. The so-called daisy brittle-star (*Ophiopholis aculeata*) is one of the most abundant echinoderms of the New England coast. Its distribution differs from that of the green sea-urchin and the sun-star only in a further extension southward on all coasts. The gaps on the North American and Siberian coasts, where specimens have not yet been taken, are conspicuous but may well be due to our imperfect knowledge of those regions. Although so very variable on the Arctic and Atlantic coasts of Europe and America that hardly two specimens are exactly alike, it is impossible to distinguish any constant varieties. In the north Pacific, however, we find not only recognizable subspecies of *aculeata,* but other species of the genus. On the American side there is a warm-water species (*bakeri*) and a cold-water species (*longispina*) which are closely related and on the Japanese side, too, there is a similar condition, with the warm-water *mirabilis* and the cold-water *brachyactis.* Differentiation into constantly distinct forms has gone further in the daisy brittle-stars (*Ophiopholis*) than in the sun-stars (Crossaster) but not quite so far perhaps as in Strongylocentrotus.

Among holothurians both *Chiridota lævis* and *Cucumaria frondosa* show peculiarities of distribution that warrant our believing their derivation and extending range correspond to those of the urchin, sea-star and brittle-star already cited. It must be said however that specific limits in these two holothurian genera are still very hazy and it is unwise in the present state of knowledge to lay any stress on evidence which they might seem to afford.

Turning now to the group of southern species, the most interesting case is the brown sea-urchin of Woods Hole (*Arbacia punctulata*). The genus Arbacia seems to have originated on the west coast of tropical America, where two species (and a third in a closely allied genus) still exist. Passing eastward during the time when there was open connection between the Pacific and the Caribbean, Arbacias finally reached the coast of Brazil, the west coast of Africa, the Mediterranean and even, far to the southeast, the isolated islet, Tristan de Cunha. But the species now occupying the Brazilian, Mediterranean and African coasts are not the same as the one which first entered the Caribbean Sea. If that one still persists, it is as *punctulata,* the Woods Hole species; if extinct now, as is quite likely, the Woods Hole Arbacia is its nearest living ally. The remarkable thing about the distribution of *punctulata* is not that it has gradually extended its range northward to the southern coasts of Massachusetts and eastward to Trinidad and Tobago, but that it seems to be entirely wanting from Jamaica and from the Lesser Antilles. It is said to occur on the northwestern coast of Cuba and there is a dubious record from Hayti, but if these records are correct, these localities no doubt received their Arbacias from the Tortugas and Florida or possibly from Yucatan. As *punctulata* has a very limited bathymetrical range, there is no reason to doubt that it has spread along shores and has not crossed wide areas of deep water. Hence the Tobago and Woods Hole Arbacias have been geographically diverging ever since their ancestors set out eastward and northeastward from the Panamic region. Yet specimens from these two extremes of the present geographical range show no characters by which one can be separated from the other even as a variety. It is interesting to note that specific limits in the genus Arbacia are very constant, and (with perhaps one exception) none of the species show very much tendency to vary. This fact is especially noteworthy in connection with the environmental changes which Arbacia endures in Vineyard Sound and Buzzards Bay. There, in severe winters, there is no question that large numbers are destroyed by cold and living specimens are rare the following summer. The survivors in a few years however replenish the region and Arbacia again becomes common. There is no evidence that this process, no doubt repeated often in a century, has as yet led to any visible, structural modifications. Arbacia, which is a relatively old type of sea-urchin, contrasts strikingly in this respect with Strongylocentrotus, a relatively recent and specialized urchin, changes in which seem to occur very easily in association with environmental changes.

One other of the southern species warrants a word because it is perhaps our commonest New England echinoderm, and its history is probably the reverse of Arbacia although, like the brown sea-urchin, it ranges from Woods Hole to Florida. This is the common sea-star of Massachusetts (*Asterias forbesi*), not the common sea-star of the Maine coast, which is *A. vulgaris* and very probably identical with *A. rubens* of Europe. Of course, it is well known that the ranges of *forbesi* and *vulgaris* overlap and it is a common belief that the two species hybridize. But if such hybrids occur they must be very rare, for there are no authentic specimens on record or extant, so far as I know. Neither do I know of any satisfactory record of the production of hybrids of the two species artificially, though it would seem to be an easy thing to do. A comparison of the distribution and habitats of *vulgaris* and *forbesi* shows clearly that *vulgaris* is a lover of cold water, while *forbesi* prefers higher temperature. So when *vulgaris* is found south of Cape Cod, it is normally only in deep, cool water (local conditions of course determine the depth) while the localities north of Cape Cod where *forbesi* occurs are shallow bays or inlets where the temperature is moderately high. So closely related are *forbesi* and *vulgaris* that young specimens can be told apart only with difficulty and by careful examination of seemingly insignificant details. It seems highly probable that *forbesi* is the direct descendant of *vulgaris;* that it is a species developed in connection with the warmer waters of the coast from Massachusetts southward. It is not necessary to assume that temperature has been a determining factor, for it may be that the range southward is due to inherent traits that permit occupation of a warmer area. In other words, the southern range may be the *result* of certain characters, rather than the *cause.* But whether cause or effect or neither, the occupation of the warmer area is associated with the fixing of certain relatively insignificant external characters, so that we recognize *forbesi* as a distinct species. No species of Asterias, *sensu strictu,* occurs south of the range of *forbesi* and its origin from the north seems therefore almost certain.

One other New England echinoderm deserves consideration as it illustrates discontinuous distribution, and represents a stage of evolution beyond that shown by Strongylocentrotus and Crossaster. This interesting case is the common synaptid of Cape Cod and Woods Hole (*Leptosynapta inhærens*), which is found not only on the New England coast, but on the northern and western coasts of Europe, on the western coast of the United States and in Japan. Comparison of specimens from Norway, Ireland, Italy, Massachusetts and California shows such close similarity among them that it seems impossible to doubt that they are all one species. Nevertheless, no Leptosynapta is known from the Arctic coasts of Asia or America and there is no reason to believe that any now occur there. What does seem probable is that, when in earlier geologic times the climate of the polar regions was mild, *inhærens* was a circumpolar species. As the climate became colder and more severe, the synaptids retreated southward along the coasts of all the continents, and those occupying the cooler areas still retain their common specific characters and we call them all *inhærens*. But on all coasts as the synaptids came into warmer waters, diversification has occurred. In European waters, four species at least have become differentiated from the original stock. On the eastern coast of America and in Bermuda and the West Indies, at least seven species have separated from each other. On the southern coasts of Japan is a well-marked species which has extended its range to East Africa on the southwest and to the Gilbert and Loyalty Islands on the southeast, while in Torres Strait another species occurs and two others occupy the southern shores of Australia.

Several other species of New England echinoderms offer interesting data regarding distribution but as each of these is similar to one or the other of the cases already cited, they need not be detailed here. The distribution of our echinoderms seems to indicate beyond doubt that, with a few noteworthy exceptions, they are of northern origin, that they have little tendency to form endemic species or varieties on our coasts, but that they are representatives of genera that in warmer seas or under more favorable conditions become differentiated into more or less numerous, constant, recognizable forms.

# SOME FACTS RELEVANT TO A DISCUSSION OF THE ORIGIN AND INHERITANCE OF SPECIFIC CHARACTERS

DR. F. B. SUMNER

SCRIPPS INSTITUTION FOR BIOLOGICAL RESEARCH, LA JOLLA, CALIFORNIA

IT seems reasonable to suppose that the geographic races or "subspecies" of mammals and birds represent early stages in the differentiation of species. The differences by which these local races are distinguished from one another appear to be of the same type as those which distinguish "true" species, and indeed the differences are, in many cases, of equally great magnitude. The assignment of a given race to the rank of a subspecies, rather than to that of a species, is due to the circumstance that it intergrades with other similar races, in all its characters, and this fact, in turn, depends entirely upon historical accident. The intergrading forms, in the one case, chance to have been preserved, in the other to have been eliminated.

When we compare the various subspecies constituting some widely ranging species, we find that they commonly differ in a considerable number of characters. In the case of mammals and birds at least, the subspecies do not differ by single characters of the presence-and-absence type, such as distinguish various "mutant" strains from one another or from the wild species. Indeed, the number of these recognizable differences commonly increases as we subject our material to more and more intensive inspection.

Furthermore, the differences under consideration are mainly of a statistical nature. While the most divergent of these subdivisions of a species may be so distinct from one another that their frequency "polygons" for certain characters show little or no overlapping, this is not true of the more closely related ones. Here, the frequency distributions for every character may overlap broadly, so that the differences must, in every case, be expressed in terms of averages. For this reason a taxonomist may hesitate to assign a given specimen to one or another "subspecies" until he is informed as to the locality from which it is taken. Such an attitude may appear unwarrantable to one who fails to recognize that subspecies are statistical and not logical concepts.

Again, the subdivision of a wide-ranging species into a definite number of geographic "subspecies" can be justified only on the further assumption that we are dealing with populations of relative homogeneity, which replace one another more or less abruptly along definite lines of demarcation. Were we concerned with one continuous population, showing insensible gradations throughout its entire range, there would be no warrant for recognizing any special number of subspecies nor for distinguishing any particular set of boundaries between their respective territories. To what extent, in general, the recognized subdivisions are arbitrary and to what extent they are natural, I am not in a position to state, nor even to form a well-grounded opinion. I may say, however, that certain test cases within my limited experience serve to give me confidence in the general validity of some of these subdivisions.

Before entering into any discussion of the nature of the differences between our subspecies, it is necessary to satisfy the natural skepticism of those who may be disposed to doubt whether we are dealing with characters which are "genetic" or hereditary at all. Many organisms are differently influenced by different environments, within the limits of the individual lifetime. May this not be true of the subspecies of mammals and birds, which inhabit regions frequently differing widely in respect to their climatic conditions? For one genus of rodents (*Peromyscus*) I have offered detailed disproof of such a contention in several previous papers,[1] and the evidence is, if possible, even more conclusive now. Several geographic races, from extremely unlike environments, have been reared together at La Jolla for from two to ten or more generations. Thus far no appreciable convergence of these types has occurred.

After one has completed the preliminary task of describing as many of these local populations as possible, with the greatest thoroughness attainable, he may feel that he has qualified himself, in a slight measure, to attack some of the various problems which arise in connection with them. Are any correlations to be discovered between these subspecific differences and factors of the environment? And aside from such correlations, is any law whatever discoverable in the arrangement of these subspecies with reference to one another? Again, do these complexes of characters which distinguish the different geographic races tend to vary together as we pass through the entire range of the species, or do the component elements change quite independently of one another? Finally, how do these subspecific characters "behave" in heredity, either in relatively pure strains of the single races, or in hybrids between different races?

The first two of these questions are ones which may be answered, in a certain measure, without recourse to breeding experiments, nor to a special mathematical technique. My own small claim to speak upon this phase of our subject is based in part upon my studies of mice of the genus *Peromyscus,* but even more upon information which I have been able to acquire through the labors of certain other students of mammals and birds.

A very little inspection suffices to show that these local races are not arranged at random. Certain general trends of geographic variation are so obvious that they have long been recognized. Among these the fore-most is doubtless the trend which seems to establish a definite positive correlation between atmospheric humidity and pigmentation. In the "Pacific Slope" area of North America, this law is evident when we pass from the relatively arid interior to the moist fog-laden atmosphere of the sea-coast. It is also evident as we pass from the coast of southern and lower California to that of Oregon, Washington and Alaska.

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[1] AMERICAN NATURALIST, November, 1915; *ibid.,* March, 1917; *ibid.,* April–May, June–July, August–September, 1918; *Journal of Experimental Zoology,* April, 1920.

This increase of pigmentation shows itself in the general darkening of the color-tone of the plumage and pelage, as well as in the expansion of the pigmented areas, and the correlative decrease in the size of the white areas. In *Peromyscus,* the darker races—at least in certain cases—are likewise found to have more pigment in various regions of the naked skin. This is true of the soles of the feet, the ears, the snout and the scrotum. On the basis of evidence which is not yet entirely adequate, I conclude provisionally that these different pigmental characters have varied together, geographically speaking. On first thought, such a situation might be regarded as an almost inevitable one, due to a seeming tendency for pigmentation, in all parts of the same individual, to vary in the same direction. That no such general tendency has been responsible for the facts will be shown to be probable later.

When we seek for a mechanism to account for this agreement between the climatic gradient and that for pigment formation, we are forced to admit that decisive evidence is not yet forthcoming. The most ready explanation at hand is the naïve one that, in some way, atmospheric humidity favors the chemical processes responsible for pigment formation. This explanation would not necessarily involve any Lamarckian assumptions as to inheritance, and furthermore it is supported by certain experimental evidence which is, it is true, very fragmentary. Reference may be made, in particular, to the experiments of Beebe,[2] in which the plumage of birds of several species was caused to become darker, apparently owing to the effects of increased atmospheric humidity; likewise to certain results of Morgan,[3] who observed several specimens of *Peromyscus* which had become very pale, as the possible result of greatly decreased humidity.

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[2] *Zoologica:* New York Zoological Society, 1907.

Such an explanation is not, however, borne out by the results of transplanting several exotic subspecies of mice to La Jolla, where, as already stated, they still maintain their characteristic color differences, even after a considerable number of generations under identical conditions of environment. Nor is it supported by the outcome of various "natural experiments" of perhaps much greater duration, which have been reported by certain naturalists. Grinnell and Swarth,[4] for example, have noted the occurrence of a subspecies of song-sparrow (*Melospiza melodia cooperi*), proper to the coastal region of southern California, which has extended its range into a canyon on the eastern (desert) slope of the San Jacinto Mountains. Yet here, in a region of great summer heat and extreme aridity, it has retained the dark plumage of the subspecies *cooperi,* and has not varied in the direction of the desert race *saltonis.*

I can not, however, regard such negative evidence as decisive in the present instance, owing to the possibility that the invading race may be continually recruited from its normal habitat on the western side of the mountains. Moreover, certain similar evidence, based upon the influx of the English sparrow into Death Valley, is at present somewhat equivocal.[5]

The chief alternative explanation of these pigmentation gradients in nature would invoke the principle of selection. We might, on the one hand, take refuge in the theory of concealing coloration, and this theory has a certain *prima facie* plausibility, particularly as applied to the pale hue of so many desert animals. I have, however, recently argued against this type of explanation, which is beset by some serious difficulties.[6] Another application of the selection principle would rest on the supposition that these varying degrees of pigmentation were, in themselves, of no service to the organism, but that they were indices of different constitutional tendencies. The type of organism best adapted to desert life might be supposed to produce little pigment, and that best adapted to coastal fogs might be supposed to produce much pigment.

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[3] *Annals N. Y. Academy of Sciences,* 1911.

[4] University of California Publications in Zoology, Vol. 10, 1913.

[5] Grinnell (unpublished Ms.)

It is obvious that a problem of this nature can only be solved experimentally. I may state that I have already commenced experiments in which the animals are being subjected to an artificial environment involving a much more extreme change of life conditions than is involved in the transplantation of exotic races to the unmodified atmosphere of La Jolla.

Some of the most conspicuous of our subspecific differences relate, however, to characters other than pigmentation. In this connection we must include not only differences in the absolute size of the body, but more particularly ones in the proportional size of various parts—the tail, feet, ears, and certain bones of the skeleton.

Here, too, we find that the various grades in the development of these parts are not arranged purely at random. There are, throughout wide expanses of territory, fairly consistent trends, in the direction of an increase or a decrease in the size of body as a whole, or in the relative size of one or another member. But, unlike the case of pigmental characters, no general law seems to be discernible here. When the data are viewed broadly, no certain correlations seem possible between differences in the proportional size of parts and definite factors of the physical environment. Indeed, contradictory tendencies may be shown by different, closely re-

[6] *Journal of Mammalogy*, May, 1921.

lated organisms, or even within different parts of the range of a single subspecies.

Although it is not the object of the present paper to discuss in detail the evidence on which the foregoing statements are made, a single illustration may be worth while. In the species *Peromyscus maniculatus,* with which my own studies have been chiefly concerned, there is a marked increase in the length (relative and absolute) of the tail and foot, as we pass northward, along the Pacific coast, from San Francisco Bay to Alaska. But from San Francisco Bay southward to the Mexican border, as well as eastward into the arid interior, the length of these members undergoes no decrease. Indeed, the mice of the Coronado Islands, near San Diego, have feet (though not tails) far longer than those of the neighboring mainland—as long, in fact, as those of mice from Humboldt Bay, at the opposite end of the state. Other erratic features in the geographic variation of these animals could be cited, even within the limits of the state of California.[7]

Facts of this class are obviously not in accord with certain generalizations which have been proposed as to the behavior of bodily proportions, in relation to climatic or geographic gradients. J. A. Allen's principle of the "enlargement of peripheral parts under high temperature or toward the tropics"[8] is certainly not applicable to the genus *Peromyscus* on the Pacific coast. Far from becoming enlarged, there is, as we have seen, a fairly steady decrease in the length of certain "peripheral parts," as we pass from Alaska to San Francisco Bay. Nor do the ears of these mice become longer, in passing either to the south or to the interior deserts, as is said to be true of various other mammals. Mice from the vicinity of Humboldt Bay in northern California were found to have ears as long as, or longer than, those from the Mojave Desert.

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[7] For birds, Swarth has recently discussed a number of groups which illustrate the independent variation of different characters geographically, as well as their inconsistent behavior in relation to climatic factors. (See especially *Proceedings of the California Academy of Sciences,* Vol. 6, 1916, University of California Publications in Zoology, Vol. 21, 1920.)

[8] Annual Report Smithsonian Institution for 1905 (1906). (Reprinted from the *Radical Review,* 1877.)

Indeed, these last named features in the geographic variation of *Peromyscus* are quite out of harmony with the supposition that they have been due to the direct action of the physical environment. My earlier experiments with white mice[9] showed that the length of the tail, feet and (doubtfully) the ears was considerably increased under the influence of high temperature and low relative humidity. If these differences among geographic races in nature depend in any way upon local differences in environmental factors, the relationships must be indirect and obscure. In the present state of our knowledge, any assertion that such relationships exist, and particularly any contention that the subspecific characters of animals are necessarily adaptive, must be dogmatic in the extreme. Indeed there are strong reasons for doubting the reality of any such nicety of adjustment as is implied in speculations of this sort.

The existence of graded series in space,[10] in cases where neither adaptive modification through selection nor the direct influence of environment seems probable, might be accounted for in two principal ways. (1) It might be supposed that, for some reason, distinct races had originated at the two points farthest removed from one another, just as they have arisen on separate islands or other regions more or less separated by barriers. Subsequently, these two races may be supposed to have diffused into the intervening territory and mixed in varying proportions through hybridization. Such a process might ultimately result in a gradation of characters throughout the entire territory involved. It would not even be necessary to assume that the intermediate tract was ever entirely devoid of a population. The two most widely separated points, owing to their offering more favorable conditions of life, might become "centers of distribution," from each of which the preponderant migration would be centrifugal.[11]

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[9] *Journal of Experimental Zoology*, Vol. 7, 1909, Vol. 18, 1915.

[10] Such series are by no means confined to mammals and birds. Gulick (Carnegie Institution Publication No. 25, 1905), in his study of Hawaiian land snails, found widely divergent species occupying points far removed from one another, these being connected, however, by numerous intermediate types. This was true in cases where corresponding environmental gradations were entirely lacking.

The only unexplained circumstance here would be the primary differentiations at the two extremes of the series, but this would not necessarily involve the assumption that the characters produced were specifically adapted to the respective habitats of these two races. On the contrary, it has been contended by a number of writers that any two small samples of a single species would, if isolated from one another, tend to develop along divergent lines, regardless of any differences in their respective habitats.

(2) We might have recourse to the principle of "orthogenesis," which, under various forms, has been espoused by a considerable number of biologists, particularly, in recent years, by paleontologists. It has been contended that a species has the same inherent tendency to vary in certain directions that a developing egg has to develop in a definite specific way. The realization of this particular trend is conceived of as being largely independent of peculiarities of the environment. Such a view would, of course, be invalidated were it shown that this apparently orthogenetic trend were the result of selection by the conditions of life. In some instances, however, such a selective process seems to be pretty definitely ruled out. Among others, may be cited those cases, already discussed, in which the same variational gradient is associated with quite different, perhaps even reversed, environmental gradients. Cases of this sort undoubtedly suggest the existence of definitely directed trends of variation. There need, however, be no ele-

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[11] Grinnell (*Auk*, July, 1904).

ment of mysticism in such a view. It is only when these directed trends of variation are assumed to make for higher development or increased adaptation that we may begin to suspect the scientific validity of such a hypothesis.

Now, some of these seemingly "orthogenetic" series appear to be arranged in space, rather than in time.[12] Cases may be cited in fact, in which the degree of modification in a given direction seems to be a linear function of the geographic distance between the races in question. It is not impossible, however, that this spatial arrangement may be fundamentally a chronological one. Thus if the manifestation of predetermined trends of variation should coincide with the dispersal of a species from some common center, we should have just such geographically graded series as we actually encounter. And this explanation would be in no way contradicted by the existence of considerable areas throughout which the characters in question were relatively stable, *i.e.*, the "ranges" of the various "subspecies."

Either of the foregoing views as to the origin of graded geographic series in nature must be regarded as highly speculative at the present time. And it must be recognized that the only thing which would be accounted for in either case would be the existence of *graded series.* Regarding the origin of the character differences themselves, we should still be completely in the dark.

The relation of such views to the modern theory of mutation should here be referred to. So far as I can learn, this theory affords no mechanism, aside from selection, competent to account for these correspondences between structural and geographic gradients. Not only are most recent mutationists very skeptical as to the specific effect of any given type of environment upon the nature of the resulting mutations, but there are reasons for doubting the efficacy of even extreme environmental changes in increasing the number of mutations *of any sort.*[13] Furthermore, it has been contended by Morgan and other writers that the various gradations in the modification of a single genetic factor do not tend to arise in any particular order. An extreme mutant condition, *f*, is as likely to arise directly from *a* as it is from *e* or from any intermediate member of the series.

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[12] Swarth ("Revision of the Avian genus *Passerella,*" University of California Publications in Zoology, Vol. 21, 1920), writing of certain races of fox-sparrows, suggests the possibility of "a predetermined line of evolution—as regards direction through space, however, rather than through time."

It may be held, however, that the varying grades of difference between these local races, in respect to any single character, depend upon the action of a varying number of cumulative ("multiple") factors, having identical or closely similar effects. If this be true, as is indeed possible, we should still have to account for the correspondence between the number of these factor differences and the distance apart of the respective races in space. This correspondence might perhaps be explained on the basis of the varying periods of time which had elapsed since the separation of the given races. Such an explanation would, however, be practically identical with the "orthogenetic" one already referred to, and would certainly be unacceptable to many mutationists.

If, therefore, we are dealing in nature, with the same class of factor changes which have been studied so intensively by the Mendelians, any correlations between these changes and environmental conditions or geographic distribution must be the result either of natural selection or of some unexplained tendency toward definitely directed variation ("orthogenesis"). But reasons may be given why selection, in some of these cases at least, is a highly improbable explanation of the facts, while the acceptance of orthogenesis would involve a radical departure from the mutation theory as originally conceived.

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[13] **Recent unpublished studies on *Drosophila*, conducted at the University of California, by Dr. Margaret Mann, greatly strengthen such doubts.**

Before proceeding further, we must give some attention to the important problem of the correlation of these various characters with one another. By correlation I here denote the tendency of two characters to vary together, either (1) in the same race, or (2) in the same individual.

Let us consider first the question: To what extent do these different characters, which are subject to local variation, tend to vary in the same or opposite directions as we pass from one race to another? Is there, in other words, any tendency for entire complexes of characters to be shifted together? As already stated, we find that the three pigmental characters of *Peromyscus* which have been subjected to quantitative determination do seem to be correlated with one another geographically. These are the general coat color, the width of the dorsal tail stripe and the depth of pigmentation of the soles of the feet. Aside from these, it seems impossible to discover any general law in the geographic behavior of the subspecific characters of these animals. Certain differential characters of the component subspecies may, it is true, undergo simultaneous change throughout a part of the range of a species, but the association between these same characters is found to be entirely dissolved when we pass to other parts of its range. It has been pointed out that the length of tail and foot in one species of *Peromyscus* increases in a parallel fashion from San Francisco Bay northward to Alaska, while elsewhere such a correlation seems to be lacking.

Secondly, we may consider *intra-individual* correlation. To what degree do these measurable characters of our animals tend to vary together *among the members of a single local race?* This is naturally of particular interest in respect to those characters which are subject to geographic variation. It must be emphasized that we are considering here correlations which are independent of the general size of the body. In a series of animals of varying size, it is needless to say, correlations will be found to exist between almost any two parts.

In an earlier paper I pointed out the existence of a well-marked intra-individual correlation between tail and foot length, and I have recently computed coefficients for certain additional pairs of characters which are involved in the subspecific differences between these mice. In these studies, both the "pure" races and hybrid material has been employed. A moderate degree of positive correlation (about 0.3) is found to exist between the shade of the pelage and the width of the tail stripe, but there is no satisfactory evidence of a correlation among any of the other characters considered. Indeed for certain pairs of characters, the evidence seems sufficient to justify the positive conclusion that no appreciable correlation exists.

Now it is possible that certain of these facts of intra-individual correlation have some bearing upon those of geographic variation. It has been pointed out that the three pigmental characters which I have measured in *Peromyscus* seem to form parallel gradients in nature, and that these gradients correspond fairly well with the climatic gradient, particularly as this relates to atmospheric humidity. The fact that two of these pigmental characters (width of tail stripe and darkness of pelage) are found to be correlated in the individual might be held to account for their coincident modification among the various subspecies. To resort to the familiar conceptions of modern genetics, these two characters might be supposed either to have, in part at least, a common factorial basis, or they might be supposed to depend upon factors which were more or less closely linked. In either case, these various coincident modifications could be regarded as manifestations of a single process of variation.

As regards the third of these pigmental characters—foot pigmentation—the evidence thus far speaks for a complete absence of correlation between this and the other two characters just referred to.[14] If this lack of correlation is rendered certain by the study of further material, and if a general correspondence with the climatic gradient is fully substantiated, we shall be forced to the conclusion that *these two characters have been independently modified along parallel lines.* Since the tendency to parallel development can not, in this case, be found within the organism itself, its source must be sought in the environment. There must be environmental agencies competent to influence (by selection or otherwise) the degree of pigment formation, regardless of the part of the body affected. On the other hand, it is plain that the existence of a correlation between two characters in the individual is not, in itself, sufficient to insure a constant correlation, geographically speaking. It has just been pointed out, for example, that an increase in the foot-length of a race may or may not be associated with an increase of tail length.

The modern student of genetics is disposed to look upon hybridization as the single fruitful method by which to attack his problems. While I can not subscribe to such an extreme view as this, I have recognized the necessity of crossing various subspecies of *Peromyscus.* Although even very widely different races yield offspring as fertile as those derived from pure races, these experiments have been beset by various technical difficulties which I can not discuss here.[15]

My chief results are based upon two series of hybrids between the most widely unlike races found in California (*rubidus* and *sonoriensis*) and one series between the more closely related *rubidus* and *gambeli.* $F_1$ and $F_2$

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[14] A positive correlation of + 0.071 was obtained. This is based upon 18 different groups of specimens aggregating 779 individuals. The separate group coefficients range from — 0.32 to + 0.47, there being 10 positive figures and 8 negative ones.

[15] These relate, in large part, to the generally detrimental effect of captivity upon wild species of mice, manifesting itself in a frequent impairment of fertility, stunting of the body, and sometimes in actual deformity.

generations were obtained, but very few back-crosses or later generations of hybrids. The resulting series have been measured and analyzed statistically in reference to the behavior of a considerable number of characters.[16]

Let me point out, before proceeding further, that none of the parent races with which I have dealt has been even approximately "pure," in the sense in which this term is customarily employed by geneticists. Each is a mixture of genetically distinct strains. As evidence of this may be cited the wide range of variability within each race, and the fact that for several different characters these variations are found to be in part hereditary. This has proved to be true of relative tail length, width of tail stripe, depth of foot pigmentation and grade of coat color, as revealed by the computation of coefficients, both for parent-offspring and fraternal correlation. The former coefficients average + 0.27, for these four characters, the latter + 0.43.[17]

This "mixed" character of the parent races employed in these crosses should not, however, affect the general significance of the results. For there would, in general, be far more factorial differences between representatives of two geographic races than between individuals of the same race. The $F_1$ generation from such a cross would present far more heterozygosis than either parent race, taken by itself, and the chances of the segregation of extreme types would therefore be much better in the $F_2$ than in the $F_1$ series.

Despite numerous exceptions and inconsistencies, the general statement may be made that both hybrid generations gave intermediate values for the various subspecific characters, while the variability on the whole was greater in the $F_2$ than the $F_1$ generation. Not only does the entire complex of characters which serves to distinguish one subspecies from another fail to behave as a simple Mendelian unit character, but the various components of these complexes—the separate characters, taken singly—fail so to behave.

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[16] A paper giving a fairly full account of the results of these experiments is now in press.

[17] It is of interest that the correlation between the $F_1$ parents and their $F_2$ offspring averages considerably *higher* than that between the parents of "pure" race and their $F_1$ offspring. Other things equal, the former coefficients should be *lower*, if we had to do with a Mendelian segregation of these characters in the $F_2$ generation. I am not, however, disposed to attach any great significance to the difference here referred to.

Now this is a picture which has often been encountered by those who have dealt with so-called "quantitative" characters in hybridization, and is the one which the well-known "multiple factor" theory was invented to explain. Indeed, it is quite certain that most geneticists will hail these results of mine as an excellent illustration of the applicability of this principle to the natural varieties of a wild species of mammal.

This may, indeed, be a correct interpretation of my results. But before reaching any settled convictions on this subject, I should strongly advise that we consider all of the evidence. Some of the awkward facts of the case are: (1) This increase in $F_2$ variability relates not only to characters in respect to which the parent races differ, but is equally evident among characters in respect to which the parent races do not differ. (2) It fails to appear in certain cases where the parent races differ widely. (3) The increase is perhaps shown most consistently in relation to a series of characters (indices of bilateral asymmetry), which, we are able to show, are not hereditary at all.[18] These results can not be adequately interpreted without considering various circumstances which it is impossible to discuss in the present paper. But they seem to furnish very doubtful support for the theory of multiple factors, as applied to the subspecific characters of these mice.

It is, of course, well known that experimental breeders before the days of Mendel fully recognized the high variability of hybrids subsequent to the first generation. But it may be contended with much truth that to substitute vague, unanalyzed tendencies of this sort for a consistent scientific explanation would be a distinct step backward. Still, it will hardly be maintained that even an erroneous explanation is better than none at all.

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[18] Sumner and Huestis, *Genetics,* September, 1921.

The upshot of my discussion, therefore, is that we are not yet prepared to frame any adequate general hypothesis as to species formation. The Mendelian-Mutation system of facts and theories appears to me to be no more successful in this respect than its predecessors. In the meantime, let us all busy ourselves with the collection of data of a sort which will be relevant to the final solution. And among these relevant data it is my belief that the facts of geographic variation will bulk as large in the end as those of Mendelian inheritance.

Let us not, however, fall into the error of supposing that the value of every discovery in this field depends solely upon its obvious bearing on the problem of evolution or the mechanism of heredity. If we do this, most of our labors will end in grievous disappointment. It is possible to arrive at results of genuine scientific importance, even if various issues, commonly regarded as fundamental, are for the time being left untouched. Prior to the present studies, no one appears to have taken the trouble even to find out how the geographic races of mammals *seem* to behave in hybridization. Imperfect or superficial knowledge is surely better than none.

# THE MITOCHONDRIA PROBLEM

IVAN E. WALLIN

THE HENRY S. DENISON RESEARCH LABORATORIES

UNIVERSITY OF COLORADO, BOULDER, COL.

THE small bacteria-like structures which may be demonstrated in the cytoplasm of all organized cells and which have come to be known as mitochondria have been recognized by biologists although their nature remains obscure. The discovery of these structures may justly be credited to Altmann (1) who believed that they are microorganisms and represent the ultimate units of life embedded in a lifeless cytoplasm of the host cell. Among others, Bütschli and Safftigen upheld a view that these structures are microorganisms having a symbiotic relationship to the host cell. A large number of investigators, however, have assumed a cytoplasmic origin of mitochondria and have preferred to consider them in the rôle of cell organs. That this latter conception has not met with universal acceptance is attested to by the brief consideration that is given to mitochondria in modern textbooks and to the varied opinions that have been advanced by numerous biologists regarding the nature of mitochondria.

In two recent papers (Wallin, 2 and 3), the writer has challenged the validity of the "microchemical" and staining methods that have been used in an attempt to establish a cytoplasmic origin for mitochondria. From the results of the experiments recorded in these papers, together with evidence by analogy therein submitted, the writer concluded that there is more evidence in favor of a microorganismal nature of mitochondria than there has been submitted in the literature to support a cytoplasmic origin of these structures. Since the publication of these papers by the writer, Cowdry and Olitsky

(4) have taken issue with the conclusions arrived at by the writer and assert: "that the discussion provoked may easily lead investigators from the main problem, which is, we take it, the elaboration of new methods for the determination of the chemical constitution of mitochondria as a prerequisite to the study of their rôle in cellular physiology and pathology." The article by Cowdry and Olitsky was followed by an unsigned editorial in the *Journal* of the American Medical Association for November 25, 1922, in which the editor exhibits an apparent unfamiliarity with the evidence in the "controversy."

It is apparent from a perusal of Cowdry and Olitsky's article and the above-mentioned editorial that certain fundamental conceptions must be clarified. These conceptions are primarily concerned with the nature of bacteria. In a previous paper, the writer (Wallin, 2) called attention to the lack of a definition of bacteria. Cowdry and Olitsky offer the following from Park and Williams' textbook on pathogenic microorganisms as a definition for bacteria: "The properties of bacteria . . . which are fairly constant under uniform conditions and which have been more or less used in systems of classification, are those of spore and capsule formation, motility (flagella formation), reactions to staining reagents; relation to temperature, to oxygen and to other food material, and, finally, their relation to fermentation and disease." To which Cowdry and Olitsky add: "the property of forming smaller or larger aggregates (colonies), the individuals of which are, however, physiologically independent (Zinsser), and the development of characteristic modes of growth on suitable artificial media." It is obvious, from the above-quoted statement, that this does not constitute a definition of bacteria nor was it, apparently, so intended by Park and Williams. A definition would include a statement of those properties that are common to *all* bacteria. It would appear unnecessary to emphasize the fact that all bacteria do not exhibit motility, spore formation and capsules, nevertheless, Cowdry and Olitsky, apparently, assume that *all* bacteria possess *all* the characteristics that Park and Williams include in their system of classification, for, to quote from their recent article: "It must be admitted in all these respects that a great gulf remains between mitochondria and bacteria. In respect to mitochondria definite spores and capsules have not been noted. The mitochondrial blebs which Wallin suggests may be due to fixation bear in our judgment no resemblance to spores. . . . Motility due to flagellar action has not been observed." It appears superfluous to emphasize that biologists in general and bacteriologists in particular have not even assumed that *all* bacteria possess capsules and exhibit motility and spore formation. The absence or presence of these properties serve as a basis for a system of classification of bacteria which in itself implies that these properties are not common to all strains of bacteria. It may appear, in the above quotation, that the writer suggested that mitochondrial blebs may bear a relationship to spores. Such a suggestion was not made by the writer, but to the contrary, he suggested that the mitochondrial blebs described by Cowdry (5) may be due to the action of chemicals just as such bleb-like appearances were produced in bacteria by the action of chemicals (Wallin, 2).

In the absence of a clear and specific definition of bacteria it is important to mention some of the properties of bacteria, particularly those properties that have a bearing on a possible relationship of mitochondria and bacteria. The probable rôle of bacteria in organic evolution has been noted by many biologists and has been clearly indicated particularly by Osborn (6). Their relationship to natural processes in the "economy of nature" is significantly illustrated in the "nitrogen cycle." Space would not permit in this article to give even an abbreviated catalogue of the more important "natural" activities that are due to bacteria. Suffice to mention such activities as the production of flavor in many of our foods, nitrogen fixation, acetic acid production, etc. The relationship of bacteria to other forms of life is varied and has been investigated chiefly from the standpoint of pathogenicity. It is well known that there are many strains of bacteria which have an intimate relationship to other forms of life, but are not necessarily pathogenic in their reactions. A suggestive and significant example of such a relationship is to be found in the *Bacillus coli* which is nourished by the food in the intestines and in turn renders the food more easily digestible by the host organism (Marshall, 7). It is only recently that this type of relationship of bacteria to higher forms of life has come to occupy the attention of investigators. Aside from a few forms like the root nodule bacteria, the symbiotic bacteria in *Psychotria bacteriophila,* and a few others, very little study has been directed toward the nature of these important life relationships.

The reactions of bacteria to stains and staining methods have also been shown to be quite varied. While the majority of free-living bacteria respond in a fairly uniform manner to the ordinary bacteriological technique, there are many strains which demand a special technique for their demonstration. Apparently, the majority of the strains which require a special technique for their demonstration are those strains that have an intimate relationship with the tissues of higher forms of life.

The cultural properties of bacteria also vary within wide limits. Here again, it appears that those forms which require very special culture media are such strains which have a symbiotic or partial symbiotic relationship to some higher form of life. In some instances an artificial culture medium has not as yet been devised which will encourage the growth of the symbiotic organism. The most significant of such organisms are the microorganisms associated with Rocky Mountain spotted fever. These organisms, whose pathogenicity and life cycle have been established by Wolbach (8) and a number of co-workers, furnish us with an undisputable example of a known microorganism which exhibits the essential characteristics of mitochondria. Briefly stated, these characteristics are: fragility, as represented by sensitiveness to acetic acid, alcohol, and mechanical manipulation; non-pathogenic in the wood tick and may be transmitted from one generation to another in the egg cell; an intracellular position in the host (apparently, also extracellular); the necessity of a special staining technique that respects their fragility. Concerning these organisms, or more particularly the organisms of typhus fever which have somewhat the same characteristics, Cowdry and Olitsky state: "In pathology these views (*i.e.*, a bacterial conception of mitochondria), if verified, would have a distinct bearing upon our conception of the significance of Rickettsia bodies in typhus fever, trench fever, and other conditions and would leave us in some doubt regarding the criteria to be employed in the identification of microorganisms the nature of which remains obscure." It may be true that a bacterial conception of mitochondria may have a bearing on the ultimate solution of the nature of Rickettsia bodies and it appears to the writer that this is not only possible, but probable. The possibility that the establishment of such a view might "leave us in some doubt regarding the criteria to be employed in the identification of microorganisms the nature of which remains obscure" is far-fetched and is quite irrelevant to the problem as Wolbach (9) has recently called attention to. The known nature, relationships and reactions of Rickettsia bodies leave no basis for any possible confusion with mitochondria, but if there were occasion for the suggested confusion the writer is convinced that *no criterion* is preferable to a *false criterion* in the search for truth.

Cowdry and Olitsky, apparently, demonstrated that mitochondria are colored in an exceedingly dilute solution (1 : 500,000) of Janus green while some six or eight different strains of bacteria which they subjected to a like dilution of the dye were unstained. Granted that Janus green in a highly diluted solution were a specific stain for mitochondria, would such a staining reaction be convincing evidence against their bacterial nature? On the basis of our knowledge concerning stains and staining reactions in general, the writer is convinced that such evidence is inconclusive. Further, Cowdry and Olitsky failed to stain mitochondria with the Giemsa stain and conclude: "The failure of this so-called nuclear dye to color mitochondria specifically points to a difference which we must consider to be fundamental between mitochondria and bacteria." The writer has definitely stained mitochondria with the Giemsa stain in smear preparations of dog fœtus tissue dried in the air and followed by absolute alcohol fixation.

It is obvious, after a broad survey of the nature of bacterial organisms, that a wide range of variations exists in the bacteria. These variations are concerned with physical and chemical properties and, of greatest significance in a bacterial conception of mitochondria, there are pronounced variations of the relationships of bacteria to other forms of life. This latter variation ranges all the way from a negative, through an indifferent and a partial symbiotic relationship, to a possible absolute symbiosis in which the bacterial symbiont is incapable of development in any natural medium with the exception of a living medium. It is apparent that, if mitochondria are of a bacterial nature, we would not expect them to exhibit the properties of hardy, free-living microorganisms, but rather the properties of such forms that have developed an absolute symbiotic relationship. Again, there are no reasons why one should assume that a bacterial mitochondrium should exhibit pathogenic properties, at least under normal conditions.

It must be borne in mind that only a small fraction of one per cent. of all bacteria are pathogenic. It must, further, be emphasized that some influence in the host cell produces a limitation of growth of the symbiotic organism. Such an influence is, apparently, present in the root nodules of leguminous plants.

The mitochondria problem is primarily concerned with a determination of the nature of these structures and is still an open problem. Further, we believe that the fundamental bearing its solution will have on the future trend of cytological investigation warrants the most thorough and exhaustive researches into the nature of mitochondria. We can not agree with Cowdry and Olitsky that biological investigators may easily be led from the main problem.

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# THE LIFE HISTORY OF THE FOUR-TOED SALAMANDER[1]

DR. FRANK N. BLANCHARD

UNIVERSITY OF MICHIGAN

THE four-toed salamander, *Hemidactylium scutatum* (Schlegel), has long been of interest because of its apparent scarcity and the obscurity of its life history as well as on account of its taxonomic isolation and relationships. It has been found from Massachusetts to Georgia and Arkansas, north through Missouri to northern Michigan, and in more or less of the intervening territory, but it has only rarely been reported as plentiful. The finding of eggs was first reported by Dr. O. P. Hay in 1892 (p. 441), who takes the word of one Mr. Hughes of Indiana to the effect that the eggs as well as the adults were "found in the moss at the roots of trees which stood near ponds." They were neither described nor preserved by the discoverer, however, nor seen by Dr. Hay. They were next found by Mr. S. C. Bishop and Prof. C. R. Crosby near McLean, New York, on May 14, 1919, while sifting for spiders, and later, May 27 and 30, numerous masses of eggs were discovered, with attendant females. These were all found imbedded in sphagnum at the bases of clumps of woody bog shrubs not more than six inches above water. Bishop (1920) followed the development of the eggs to hatching, and to what he considered the beginning of resorption of the gills six days later. Then his last specimens died.

Three years later, May 13, 1922, eggs were discovered near Ann Arbor by the writer in exactly such a situation as described by Dr. Hay thirty years ago. Eggs were found in three widely separated localities (Lima, Iosco, and Whitoak townships) within 12 to 30 miles of Ann Arbor, and at the latter of these places in great abundance. Evidence from these collections and much other field work in this vicinity indicates that the eggs of *Hemidactylium* may be expected anywhere in this region where ponds, pools or swamps lie in, or directly adjacent to, deciduous woods, and are so shaded as to support a good growth of mosses or soft rotted wood directly at the water's edge. For it is in such moss, entangled in the rhizoids, or in damp cavities in soft, rotted wood, nearly or quite directly over free water, and from 2½ to 7 inches above the water, that the egg clusters have been found, and almost without exception with an attendant female.

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[1] Contribution from the Zoological Laboratory of the University of Michigan.

Adult and juvenile four-toed salamanders have been taken by the writer in eight other localities in this region (in the townships of Milford, Scio, Freedom, Pittsfield, Sylvan, Waterloo, Norvell and Hamburg) and in each instance there is a suitable breeding site in the immediate vicinity. Much hunting in many other localities where only one of the two conditions—suitable breeding site and deciduous woods—were present, has so far failed to disclose either young or adults.

The details of breeding behavior and egg deposition have yet to be found out. It may be supposed, however, that fertilization is in some way by means of spermatophores. The adults swim well but only with effort, and cannot live long in water unless there is opportunity for resting at the surface. It is certain, however, that the females take to the water voluntarily, for they were several times found with eggs in clumps of grass and mosses away from shore. The eggs found by Bishop on May 14 were in the neural fold stage, and had probably been deposited about three days. He observed that it took 19 days from that stage to the development of gill and fore limb buds—the condition in which they were first found in Michigan, on May 13th last. Reckoning back 22 days from May 13 gives April 19 as the approximate date of deposition of eggs near Ann Arbor.

Hatching was observed to take place in the field on May 27, but eggs which on May 13 were no further advanced than those left in the field, hatched in the laboratory four days earlier. It was observed also that eggs kept in water hatched earlier than eggs kept in damp moss. Thus temperature and moisture, and probably other factors, have a direct influence on the period of incubation. But the normal time from egg deposition to hatching figured approximately 38 days. (Bishop found it about 30 in his individuals reared in the laboratory.)

Whether the larvæ of *Hemidactylium* normally enter the water for a portion of their development has never been settled. Evidence bearing directly upon this point is contained in observations on the hatching of a mass of eggs on May 27, 1922. The eggs were at the base of a clump of red-osier dogwood, 2½ inches above water, under a thin moss covering in a few grass roots and some moss rhizoids. An adult female was present. When the female was picked up a larva was sticking to her tail. Two larvæ were noted free from the jelly envelopes, and one had only its head remaining in the jelly. These and several others were found loose in the wet jelly, which may have been partially squeezed by my hand pressing the moss in first opening the nest. One larva was found within 1½ inches of the water, to which a wiggle or two would have brought him. The one with his head caught experienced great difficulty in getting free, but finally did so and then lay for a time in contact with the somewhat sticky mass. Wrigglings at intervals of a few seconds afforded sometimes a little, sometimes no progress, until a stronger wriggle set him free, and he flopped the full three inches into the water below. Two more were watched as they freed themselves head first from their jellies. One made many flops but still stuck by surface tension and the adhesiveness of the jelly, while the wriggles became less frequent. Finally, however, he became free from the jelly and began to make progress downward. In a recess unaltered by my disturbance of the nest, I watched three larvæ wriggle down to the water. Progress was plainly much easier when free from the sticky jelly and from contact with other larvæ. Several others were watched as they emerged from the eggs and made towards the water. Of the movements that assisted in this progression, some were mere bendings or turnings of the body, others, when horizontal, were like swimming movements, still others were violent wrigglings of the whole body. They appeared to be merely continuations of the movements that all amphibian larvæ make long before free from their jelly envelopes. That these movements led the young four-toed salamanders to their proper environment can scarcely be doubted. Looking down into the water near eggs that had been hatching, I saw one of the newly hatched larvæ above a dead leaf just under the surface of the water. A moment later it had disappeared. With a dip net several larvæ of the same size were taken near the dogwood clump. These larvæ and others secured with a dip net in the same pond at later dates were taken to the laboratory.

To test the theory that the larvæ never enter the water, or do not necessarily enter it, but undergo a short development and transformation in the moss, several dishes were provided with damp moss and eggs nearly ready to hatch, and covered. Controls were kept with free water in the bottoms of the dishes. Lack of time and imperfect technique prevented satisfactory results, but the indications were as follows: (1) larvæ will readily live from 10 to 16 days in no more water than enough to keep their bodies wet, but during this time there is no apparent growth and little if any reduction of the gills; (2) the larvæ do not stay in the moss, but on hatching reach the bottom of the dish and stay there; (3) there is no evident avoidance of a source of light and possibly an attraction toward it. Without doubt much can be learned about the larvæ of *Hemidactylium* from carefully conducted experiments.

A study of development in the laboratory was largely unsuccessful because of the difficulty of providing a constant and sufficient supply of food. The young salamanders were observed to feed readily upon rotifers and entomostracans. When these passed very close to the quiet larva a sudden snap of the head and jaws rarely failed of a capture. Always, however, the individuals reared in the laboratory were smaller and thinner than those fresh from the ponds. They developed limbs and fingers, it is true, and the limbs came gradually from a merely stick-like supportive function to be used for walking upon the bottom, but normal development undoubtedly depends upon the essentials of a natural environment, *i.e.*, suitable temperature and light, clean pond water, and plenty of small organisms that can be used as food. Furthermore, only one or but very few individuals should be kept in a single aquarium, as when many are kept in close quarters they bite off each other's gills.

MEASUREMENTS IN MILLIMETERS OF JUVENILES OF HEMIDACTYLIUM SCUTATUM.

*Larvæ*

Time of Collection

| June 11 | | | June 16 | | | June 25 | | | July 2 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Body[1] | Tail[1] | Tail / Body | Body | Tail | Tail / Body | Body | Tail | Tail / Body | Body | Tail | Tail / Body |
| 10.0 | 8.0 | .80 | 10.0 | 7.8 | .78 | 10.7 | 8.3 | .77 | 11.0 | 6.3 | .57 |
| | | | 10.0 | 7.8 | .78 | 10.9 | 8.0 | .73 | | | |
| 10.0 | 7.8 | .78 | 11.0 | 8.1 | .74 | 11.0 | 8.8 | .80 | | | |
| | | | 11.8 | 9.6 | .81 | | | | | | |

*Subadults*

| | Time of Collection | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | July 30 | | | Aug. 20 | | | Nov. 5 and 7 | | |
| | Body | Tail | Tail / Body | Body | Tail | Tail / Body | Body | Tail | Tail / Body |
| | 11.5 | 7.0 | .60 | 11.9 | 6.9 | .58 | 17.5 | 16.4 | .94 |
| | 12.9 | 9.0 | .69 | 13.7 | 8.1 | .59 | 18.1 | 17.2 | .95 |
| | 13.5 | 9.2 | .68 | 14.0 | 9.5 | .68 | 19.0 | 13.6 | .71 |
| | 13.8 | 9.5 | .68 | 14.0 | 11.2 | .80 | 19.5 | 17.0 | .85 |
| | 14.0 | 11.0 | .78 | 14.0 | 11.5 | .82 | 19.5 | 20.8 | 1.07 |
| | | | | 14.9 | 8.8 | .58 | 20.5 | 19.1 | .93 |
| | | | | 14.9 | 10.9 | .73 | 21.0 | 19.0 | .90 |
| | | | | 17.0 | 15.5 | .91 | 21.3 | — | — |
| Average...... | 13.1 | | .69 | 14.3 | | .71 | 19.6 | | .91 |

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[1] Body length is measured from tip of snout to just behind the hind leg; the length of the tail is measured from that point to its tip.

Something of development under natural conditions is shown by collections of larvæ in the same pond (Lima township) on June 11, 16, 25, and July 2, and of sub-adults at other places on July 30, Aug. 20, and Nov. 5 and 7.

The specimens collected in June showed only slight differences, but the one taken on July 2, although possessing practically full-sized gills, was distinctly less slender in body and had a noticeably reduced tail. That no collections could be made between July 2 and July 30 is unfortunate, for between these dates the transformation took place. Judging from the state of development of the specimen collected on July 2 and the probable date of drying up of the pond, it may be supposed that transformation took place a little before the middle of July. On July 30 the pond was dry, except for the mud below the superficial dry crust. Search in the moss and grass directly at the edge of the pond revealed five isolated sub-adults, with conspicuously short tails, practically without constrictions, with a black patch on each side of the head showing the position of closure of the gill slits, and with a horizontal black line through the eye (a characteristic of the larva) still conspicuous. On August 20, eight specimens collected under pieces of wood in the shady portion of another dry pond showed increasing size of body, slightly greater proportionate tail length, fainter black gill patches, and, for the most part, faintly indicated caudal constrictions. Those collected in November had longer tails (still much shorter than in adults), no gill patches, well-developed caudal constrictions, but still rather prominent dark postocular lines. Adults, however, often show these lines, although inconspicuously.

These notes are but fragmentary, it is fully realized, but it may be assumed that they prepare the way for a complete life history of this interesting salamander. The story to date may be summarized as follows:

1. The eggs are laid, in the vicinity of Ann Arbor,

about the middle of April or a little later, in clusters imbedded in the rhizoids of moss and roots of grass from 2½ to 7 inches above water.

2. Eggs will not be found unless the breeding site is directly adjacent to a piece of wooded land, nor will adults be found in woods not adjacent to a suitable breeding site.
3. The period from egg deposition to hatching is about five weeks.
4. There is an aquatic larval life of about six weeks.
5. The newly transformed individuals have dark gill patches, a dark line extending from the snout to behind the eye, and disproportionately short tails without basal constrictions.
6. Development during the rest of the season results in obliteration of the dark gill patches, a slight fading of the postocular line, the development of the caudal constrictions characteristic of the adult, and an increase in the proportional length of the tail.
7. The fully adult form and sexual maturity are not attained the first season.

## ACKNOWLEDGMENTS

The writer wishes to express his thanks to Miss Doris M. Cochran, of the Division of Reptiles, United States National Museum, for a list of the specimens of *Hemidactylium scutatum* in the collections under her care, and his indebtedness to Dr. Frieda Cobb Blanchard for much assistance in the field work.

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# THE DEVELOPMENT OF ASYMMETRY IN THE FIDDLER CRAB

## PROFESSOR T. H. MORGAN

THE experiments of Przibram ('01, '07, '17) and of others have shown in certain species of decapod crustaceans, in which a larger and a smaller "claw" are normally present, that after the removal of the large claw the smaller claw develops into a large claw. In other species, however, including the fiddler crab (*Gelasimus*), this renewal does not take place after the removal of the large claw. A new large claw regenerates on the stump of the old one.

It was known (Hyman, 1920) that in the earliest stages of the fiddler following the Zoea the two claws (first pair of legs) are equal in size and in shape and are like those of the female or like the small claw of the male. I tried to find out whether, if one claw is removed from young male crabs in these undifferentiated stages, the remaining claw will develop into a large claw.

It was necessary first to find at what stage the difference in size of the two claws first appears in the young crabs. Here a new fact of some interest came to light. Collections of young crabs were made at North Falmouth, Massachusetts, on July 10, August 3, September 2 and 15, 1922. Those collected on July 10 were crabs of the preceding summer and will be described later. A new generation came to land in August and September and those of September 2 and 15 give the results shown in the following table. The crabs fall into three groups: (1) those with unequal claws ("male" and "female" claws, or else juvenile, Fig. 1, *c;* and Fig. 2, *b;* and Fig. 3,

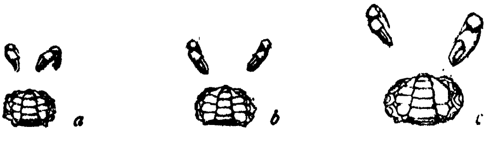

FIG. 1. Young crabs 2, 2¼ and 3 mm. across carapace, with narrow abdomens; *a* and *b* have equal small claws; *c*, left claw "large."

*a*), (2) those with small claws of equal size ("female" or else juvenile, Fig. 1, *a* and *b;* and Fig. 2, *a*), (3) those with two large claws of "male" type (Fig. 3, *b* and *c*, *c'*).

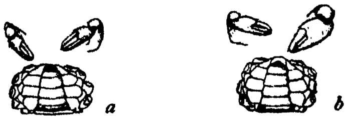

FIG. 2. Young crabs (3½ mm.) with narrow abdomens; *a*, has equal small claws; *b* has left claw large.

| | | |
|---|---|---|
| Nine crabs with unequal claws .......... | 1 | 3½ mm. across carapace |
| | 1 | 3 mm. across carapace |
| | 4 | 2½ mm. across carapace |
| | 3 | 2 mm. across carapace |
| One hundred crabs with equal, small claws . | 1 | 4½ mm. across carapace |
| | 2 | 4 mm. across carapace |
| | 4 | 3½ mm. across carapace |
| | 35 | 3 mm. across carapace |
| | 25 | 2½ mm. across carapace |
| | 32 | 2 mm. across carapace |
| | 1 | 1½[1] mm. across carapace |
| Fifty-six crabs with two large claws. ...... | 3 | 4 mm. across carapace |
| | 4 | 3½ mm. across carapace |
| | 20 | 3 mm. across carapace |
| | 29 | 2½ mm. across carapace |

It is obvious from this table that a difference in size sufficient to indicate the male type may appear in a few crabs whose carapace measures only 2 to 3 mm. in cross diameter. There were only 9 individuals that showed this male differentiation in the first lot of the table. There were 100 crabs whose carapace measured from 1½ to 4½ mm. with small equal claws. These include all the young female crabs but probably a certain number of males that had not yet shown the male type of claw.

In addition there were 56 crabs whose carapace measured from 2½ to 4 mm. *with two large claws* (male type, Fig. 3, *b* and *c*). These are undoubtedly males that have male claws on both sides. The large number of these crabs seems to indicate that many of the males pass through a symmetrical stage in which both claws have

[1] Below limit of expected change.

the male type. Since such a condition is extraordinarily rare in the adult males—only two cases having been so far recorded—it seems to follow that at a later stage these males must become asymmetrical by the reduction of one of the claws. It was too late in the season to follow up this interesting result, but I hope to study this relation further next summer.

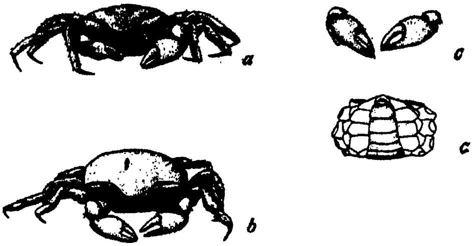

FIG. 3. Crabs (4 mm.); *a* has unequal claws, left large; *b* and *c* have equal large claws; *c′*, abdomen of *c*.

## OPERATION ON YOUNG MALES

The first experiments were with the young male crabs collected July 10. The carapace measured from 5 to 7 mm. and the two claws differed not only in size but the large claw had the shape characteristic of the male claw (Fig. 4, *b*). In 56 cases (*A*) the large claw was on the left side; in 35 cases (*B*) it was on the right side.

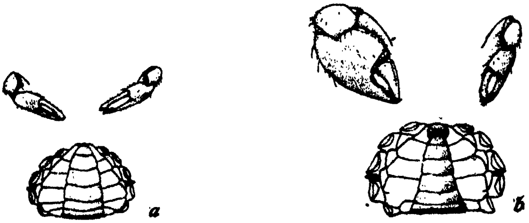

FIG. 4. Female and male crabs (5 mm.); *a*, female with equal claws; *b*, male with right claw large.

(*A*) After removing the large left claw the crabs were kept until the next molt. Six were lost, six died, the remaining 44 all regenerated a large left claw in place of the large left claw removed.

(*B*) After removing the large right claw all 35 regenerated a large right claw in place of the large right claw removed. It is evident that when the young male crabs have reached a stage in which the two claws have become differentiated, no transfer takes place when the large claw is removed. This is also what happens in the adult crabs.[2]

One claw was removed from young crabs with equal claws that were presumably females (Fig. 4, *a*). In 13 cases (*A*) the left claw was removed; in 17 cases (*B*) the right claw was removed.

(*A*) After the first molt 12 crabs regenerated a new small claw like the one removed. The other claw remained small. In one case a "male" claw developed on the right side. This individual obviously was a male in which the two claws were still equal in size when the operation was carried out. It was the smallest crab present (about 3½ mm.).

(*B*) After the first molt 4 had died, 2 were lost and 10 regenerated a small claw in place of the small claw removed. One regenerated incompletely, but although the left claw was the larger it was not much larger, or in shape like a male claw.

It is clear from these results that if the removal of one claw of the male is to have any influence on the development of the remaining claw it must be removed at an earlier stage, perhaps before the claws have shown a natural difference in size. Operations were then carried out on some of the young crabs collected in August. These were crabs of that year.

Only the smaller crabs were used in which the two claws were seen to be small and alike. The left claw was removed in all cases. The crabs were separated into three lots according to the approximate width of the carapace. As the following table shows, the six smallest crabs were too small to show a differentiation even after the next molt but those of the second and third sizes give a positive result.

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[2] Of 524 adult male fiddlers, 241 had right claw large, and 283 had left claw large.

| LEFT CLAW REMOVED | AFTER MOLT |
|---|---|
| Size 1. (1 to 1½ mm.) 6 crabs. | Both claws small. |
| Size 2. (2 mm.) 18 crabs ........ | 10 had both claws small.<br>8 had right claw large. |
| Size 3. (2½ to 3½ mm.) 25 crabs. | 12 had both claws small<br>13 had right claw large. |

Of the 18 crabs of the second size (2 mm.) 10 regenerated a small left claw, and in 8 crabs the new right claw was larger and typically male-like.

Of the 25 crabs of the third size (2½ to 3½ mm.) 12 regenerated equal claws after the first molt. Three of these were kept through a second molt. Both claws remained small. The remaining 13 crabs of this third size regenerated a right large claw. Six of these were kept through a second molt and still showed only one (right) large claw.

Since it was not possible to distinguish males from females in these young crabs it is to be expected that about half of the crabs were female, hence for these no enlargement of the new or of the remaining claws is expected. The other half are expected to be male crabs and here a change is possible. It is significant, therefore, to note that about half of the crabs developed a large right claw and none developed a large left claw in place of the one removed. The numbers are regrettably small and there is the further complication that at the stage these crabs have reached after the first molt and perhaps even after two molts there are two large claws even in normal male crabs. It can not be asserted, therefore, that a permanent development of a male claw has taken place as a result of the operation but it seems not improbable that the induced development would lead to the permanent asymmetry of the crab claws.

# FURTHER EVIDENCE ON VARIATION IN THE WIDTH OF THE ABDOMEN IN IMMATURE FIDDLER CRABS

PROFESSOR T. H. MORGAN

In an account of some variations in secondary sexual characters of fiddler crabs (The American Naturalist, LIV, 1920) I described and figured several cases in which the abdomens of a few females were narrower than in other individuals of the same size and in this respect might be interpreted either as a variation in the female in the direction of the male type or else as a partial retention of a juvenile condition of the abdomen. After discussing the pros and cons of the situation I concluded that these crabs showed "an apparent change towards maleness or possibly a retention of the juvenile condition." . . . "These questions must be further investigated before a decision can be reached." The following account is a further attempt to discuss the nature of this variation in the width of abdomen of the exceptional cases reported in my former paper. Miss Rathbun (The American Naturalist, LV, '21) criticized my conclusion on the grounds that I offered no evidence to prove that the individuals in question were not simply juvenile stages through which the female fiddler normally passes. Miss Rathbun also stated that verification of her interpretation could be obtained from one of the Californian crabs, *Hemigrapsus nudus*. Fortunately I was able during the winter and spring of 1921 to collect and examine some of these crabs as well as young stages of two other Pacific Coast species. Miss Rathbun also pointed out that in the absence of measurements of the crabs described in my paper and owing to lack of knowledge of the juvenile stages of fiddler crabs it was not possible to determine to what extent the results were exceptional.

As will be shown the stages I described do overlap at one end the juvenile stage, but most of the crabs with narrow abdomens that I referred to occur at a stage when most of the crabs have, as I stated, an abdomen that has its full width. They, therefore, represent, as I supposed, a variation in a secondary sexual character. As the crabs from which the drawings were made are still preserved I can now give their measurements and in addition I can also give the size and condition of the abdomen of fiddler crabs of the same size as well as the relative width of the abdomen both in larger and in smaller crabs.

The fiddlers on which the first part of this paper is based were collected by Miss Phoebe Reed at Pt. Pleasant, N. J., and by Mr. Wm. Procter at Cataumet, Mass. The California crabs were collected by myself from the lower end of San Francisco Bay near Palo Alto, and on the coast north of Half Moon Bay. The measurements have been made by Miss Phoebe Reed, to whose skillful assistance I am greatly indebted. A description of the zoea and megalops stage and of the earliest crab stage that succeed the free swimming stage has recently been given by O. W. Hyman. The oldest stages figured seem to correspond to the youngest stage of my material.

In the earliest crab stage of the fiddler the abdomens of males and females are both narrow and extremely alike. On the innermost surface the rudiments of the appendages are present but it is difficult to distinguish the male from the female condition. It is easier to determine the sex in all except the first two or three stages, by the difference in size of the "claws." This difference is often present in crabs measuring 3 mm. across the thorax. In Table I, crabs having the same width of abdomen are placed in the same vertical column. The width of the carapace of the same crabs is given in the horizontal line. How far the abdomen fails to cover the ventral surface of the crab (*i.e.*, how far it falls short of the bases of the legs) is not apparent from this table and calls for a further statement.

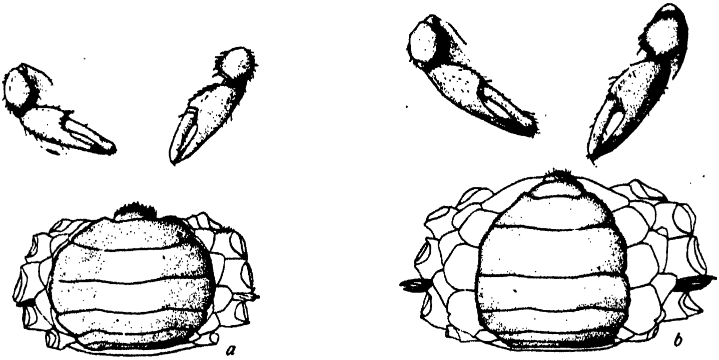

FIG. 1. *a*, female (10 mm.) with abdomen (6 mm.) full width; *b*, female (11 mm.) with abdomen (5½ mm.) less than full width.

## TABLE I

| Carapace width mm. / Abdomen width mm. | 4 | 4½ | 5 | 5½ | 6 | 6½ | 7 | 7½ | 8 | 8½ | 9 | 9½ | 10 | 10½ | 11 | 11½ | 12 | 12½ | 13 | 13½ | 14 | 14½ | 15 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | | 1 | | | | | | | | | | | | | | | | | | | | | |
| 1½ | 2 | 1 | 3 | | | | | | | | | | | | | | | | | | | | |
| 2 | | | 6 | 2 | 4 | 1 | ♂ | | ♂ | | | | | | | | | | | | | | |
| 2½ | | | | | 1 | 3 | 4 | 2 | ♂ | | | | | | | | | | | | | | |
| 3 | | | | | | 1 | 6 | 9 | 5 | 2 | | | | | | | | | | | | | |
| 3½ | | | | | | | | 1 | 9 | 3 | | | | | | | | | | | | | |
| 4 | | | | | | | | | 5 | 4 | 5 | 1 | | | | | | | | | | | |
| 4½ | | | | | | | | | | 2 | 6 | 3 | 1 | | | | | | | | | | |
| 5 | | | | | | | | | | 1 | 7 | 3 | 1 | 1 | | | | | | | | | |
| 5½ | | | | | | | | | | 1 | 7 | 6 | 5 | 2 | 1 | | | | | | | | |
| 6 | | | | | | | | | | | 2 | 6 | 21 | 5 | 1 | | | | | | | | |
| 6½ | | | | | | | | | | | | | 10 | 10 | 5 | 1 | | | | | | | |
| 7 | | | | | | | | | | | | | 13 | 13 | 22 | 7 | 2 | 1 | | | | | |
| 7½ | | | | | | | | | | | | | 1 | 5 | 14 | 10 | 6 | | 1 | | | | |
| 8 | | | | | | | | | | | | | | | 3 | 12 | 31 | 10 | 5 | | | | |
| 8½ | | | | | | | | | | | | | | | | 4 | 12 | 7 | 2 | | 1 | | |
| 9 | | | | | | | | | | | | | | | | | 6 | 3 | 15 | 6 | 6 | | |

FIDDLER CRABS—♀, *Uca pugnax* (?)

The following partial summary of this table gives the necessary information concerning the condition of the abdomen whether full width or less. Crabs whose breadth was 8½ mm. showed the following conditions. The abdomen of one crab was full width (5½ mm.); in twelve others it was not full size (5 mm., 4½, 4, 3½ and 3).

At 9 mm. two crabs had a full width abdomen (6 mm.); in seven it was 5½ mm., *i.e.*, not quite full breadth; in seven it was 5 mm.; in six it was 4½ mm. (see Fig. 5*A* in earlier paper); and in five it was 4 mm.

At 9½ mm. six crabs out of nineteen had an abdomen 6 mm., *i.e.*, nearly full breadth; in six it was 5½ mm. (see Fig. 5*B* in earlier paper); in three it was 5; in three it was 4½ and in one it was 4 mm.

At 10 mm. the broadest abdomen was full width (7½ mm.); in thirteen it was 7 mm.; in ten it was 6½; in twenty-one it was 6 mm. (like that in Fig. 1, *a;* or Fig. 5*B*. in earlier paper); in five it was 5½ mm.; in one it was 5 and in one (2d molt) it was 4½ (one of the variations of earlier paper, *viz.*, Fig. 5*B*).

At 10½ mm. there were five crabs with an abdomen 7½ mm.; thirteen with abdomen 7 mm. (like Fig. 5*B* in earlier paper); ten with 6½ mm.; five with 6 mm.; two with 5½; and one with 5 mm.

At 11 mm. there were three crabs with abdomen 8 mm.; fourteen with 7½ mm.; twenty-two with 7 mm. (two of these had eggs); five with 6½ mm.; one with 6 mm. (like Fig. 5*C* in earlier paper) and in its first skin measured 5½ mm. (Fig. 1, *b*).

In crabs larger than these, relatively less variation was observed and in practically all of them the abdomens would be set down as full breadth, if a little leeway be allowed.

It is evident from the measurements that crabs 8½ to 10½ mm. across the carapace include those stages in which the abdomen becomes as a rule full width. Abdomens of full width may be found in crabs 8½ mm., and this occurs in increasing frequency in the following "stages" yet in each a few crabs are found whose abdomens are less than full width. It is from the latter group (with one exception) that those figured in my previous paper were taken. It is fairly evident that the condition is due to the failure of the abdomen in some young crabs to attain the full breadth characteristic of the adult females, and in this respect they may be said to retain for a time a more juvenile stage common to both sexes, which stages are more like those of the adult male than like those of the adult female.

How far crabs of a given size represent the same stage in development is not evident from these results. In general successive stages show a measurable size difference, *i.e.*, there is an abrupt increase in size after each molt that comes quickly to an end as the cuticle hardens. On the other hand from the evidence that I have obtained from crabs kept in confinement there may be no increase in size after a molt. Presumably this is due to insufficient food, or to some other condition in the environment. If such conditions occur at times also in nature, then size is not always an accurate measure of age. Whether the abdomen would be more likely to retain its juvenile proportions if the crabs do not grow between molts is not known, but I had already obtained evidence that showed that such a failure does sometimes occur. For example, I kept most of the female crabs with narrow abdomens in dishes of water in the laboratory, feeding them almost daily on as much food (clams and mussels) as they would take. Several were kept till the next molt had occurred, and two, at least, through two molts. In these the abdomen did not increase in width or only slightly so, but these crabs themselves increased in size very slightly or not at all. While I was formerly somewhat more inclined to interpret this result as evidence showing that the variation might be something more definite than retention of the juvenile stage, I am inclined now to think that the evidence is not sufficient to show this, but rather that the result was due to the failure of the crabs to increase to the normal extent and that the result is correlated with the retention of the more juvenile condition of the abdomen. If, under natural conditions, such influences prevail at times we may find a partial explanation of the retention of the narrow abdomen in crabs of an age (in time) when a full width abdomen is normally attained.

### JUVENILE STAGES OF *Hemigrapsus oregonensis*

These crabs (1074 females and 1028 males) were collected in the lower end of San Francisco Bay. Rough measurements made at the time gave the following results. The females measure from 6 to 22 mm. in breadth of carapace and the males from 5 to 25 mm. Amongst the females the smallest crab with abdomen of full width measured about 9 mm. There were seven others in this class with narrower abdomens. Amongst the 10 mm. class, ten had full width abdomens and 23 narrower. Amongst the 12 mm. class, 143 had full width and 16 narrower abdomens. Amongst the 13 mm. class, 244 had full width and 5 narrower (not quite full) abdomens. All others above the last size had full width abdomens.

More accurate measurements of some of these crabs that were made later gave the data in Table II.

The change to full width abdomen took place between 10 and 12 mm. in many of the crabs. There was one 12 mm. with abdomen 9 mm. (full width), two with abdomens not quite full (8½ mm.) and two with distinctly narrower abdomens (6½ and 7 mm.). At 12½ mm. there were 2 with abdomens 9 mm., one crab with nearly full width abdomen (8½ mm.), one with abdomen 7½ and one only 7 mm. The greatest amount of variation in width of abdomen is found in the classes whose carapace measures 9, 9½, 10, 10½ and 11 mm., *i.e.*, at about the time of transformation into the broad type.

It is interesting to note that in one case a crab measuring 8 mm. with a narrow abdomen (4 mm.) carried eggs; five crabs measuring 10 mm. with abdomens 6, 6½,

TABLE II

| Carapace width mm / Abdomen width mm. | 7 | 7½ | 8 | 8½ | 9 | 9½ | 10 | 10½ | 11 | 11½ | 12 | 12½ | 13 | 13½ | 14 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 3 | 2 | | | | | | | | | | | | | | |
| 3½ | 3 | 2 | 1 | | | | | | | | | | | | |
| 4 | 1 | | 6 | | 1 | | | | | | | | | | |
| 4½ | | | 3 | 5 | 2 | | | | | | | | | | |
| 5 | | | 1 | 2 | 6 | 2 | 1 | | | | | | | | |
| 5½ | | | | | 1 | 2 | 3 | 1 | | | | | | | |
| 6 | | | | | 2 | | 1 | 1 | 1 | | | | | | |
| 6½ | | | | | 4 | 2 | 2 | 1 | 2 | 2 | 1 | | | | |
| 7 | | | | | | | 3 | 2 | 1 | | 1 | 1 | | | |
| 7½ | | | | | | | 1 | | 2 | | | 1 | | | |
| 8 | | | | | | | | 1 | 1 | 2 | | | | | |
| 8½ | | | | | | | | | | | 2 | 1 | | | |
| 9 | | | | | | | | | | | 1 | 2 | 1 | | |
| 9½ | | | | | | | | | | | | | | | |
| 10 | | | | | | | | | | | | | | | |

Shore Crabs, *Hemigrapsus oregonensis*, ♀♀

6½, 7 and 7½ mm. also carried eggs; another 10½ mm. (with abdomen 7 mm.) carried eggs; while another 11 mm. (abdomen 7) also carried eggs. The results show that these crabs may become sexually mature before the abdomen has fully attained its characteristic female shape. It may be added that amongst the crabs of these same sizes with abdomens full breadth there were also 23 that carried eggs on the abdomen.

## Juvenile Stages of *Hemigrapsus nudus*

The crabs (159 females and 122 males) were collected in the spring of 1921. The females that were measured ranged from 14 to 30 mm. in width of carapace and the males from 9 to 30 mm. Forty female crabs were picked out as showing somewhat narrow abdomens (measuring from 14 to 20 mm.). See Table III.

TABLE III

| Carapace width mm. / Abdomen width | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2 | | | | | | | | | | | | | | | |
| 3 | | 3 | 1 | | | | | | | | | | | | |
| 4 | | 1 | 3 | 6 | | | | | | | | | | | |
| 5 | | | 1 | 1 | 5 | 1 | | | | | | | | | |
| 6 | | | | | | 4 | 3 | | | | | | | | |
| 7 | | | | | | | | 8 | 3 | | | | | | |
| 8 | | | | | | | | 2 | 6 | 3 | 1 | | | | |
| 9 | | | | | | | | 1 | 1 | 10 | 2 | 1 | | | |
| 10 | | | | | | | | | 1 | 5 | 7 | 2 | | | |
| 11 | | | | | | | | | | 1 | 3 | 3 | | | |
| 12 | | | | | | | | | | | | 3 | 1 | 2 | |
| 13 | | | | | | | | | | | | | | 3 | 1 |
| 14 | | | | | | | | | | | | | | | |
| 15 | | | | | | | | | | | | | | | 1 |
| 16 | | | | | | | | | | | | | | | |

Rock Crabs, *H. nudus*, ♀♀

The table shows that in the 14, 15, 16, 17 and 18 mm. classes some crabs had abdomens that were full width, while in the same classes there were also crabs whose abdomens were one, two, or three millimeters less than full width. If these millimeter differences in width of carapace correspond even approximately to different molting stages, it appears that some crabs attain the full width of abdomen when they are much smaller than others, or stated conversely, a few crabs do not have full width abdomens, although they are larger than others that have reached this condition.

## Juvenile Stages of *Pachygrapsus crassipes*

The crabs (38 females and 40 males) were collected with the last species. The females that were measured ranged from 14 to 35 mm. in width of carapace and the males from 13 to 40 mm. Table IV gives the measurements.

TABLE IV

| Carapace width mm. / Abdomen width mm. | 18½ | 19 | 19½ | 20 | 20½ | 21 | 21½ | 22 | 22½ | 23 | 23½ | 24 | 24½ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 9 | | 1 | | | | | | | | | | | |
| 9½ | | | | | | | | | | | | | |
| 10 | | | 1 | | | 1 | | | | | | | |
| 10½ | | | | | | | | | | | | | |
| 11 | | 1 | 1 | | | 1 | | | | | | | |
| 11½ | | | | | | | | | | | | | |
| 12 | | | 2 | 1 | | | | | | | | | |
| 12½ | | | | | | 2 | | | | | | | |
| 13 | | | | | | | | | | 1 | | | |
| 13½ | | | | | | 1 | | | | | | | |
| 14 | | | | | | | | | | | | | |
| 14½ | | | | | | | | | | 1 | | | |
| 15 | | | | | | | 1 | | | 1 | | 1 | |

Rock Crabs Rippled, *Pachygrapsus crassipes*

At 19 mm. one crab had abdomen full width (11 mm.). In each of the classes, 19½, 21, 23 mm., there were crabs whose abdomens were full width, but in each there were one or two crabs whose abdomens were one, two, or three mm. less than the former. Above 24 mm. all crabs had abdomens full width.

## Conclusions

Examination of four species of young crabs shows that at first the abdomen is narrow both in the male and female. In the fiddler the abdomen is still narrow in female crabs at a time when the first pair of claws of the male show that secondary sexual differences have already appeared. Later a certain stage is reached when the abdomen of the young females becomes much wider than that of the male; but not all the crabs of a given size in this period attain the full width of abdomen and in one species a few crabs may even become sexually mature with an abdomen less than full width.

It is clear from the results that at the time when the narrow abdomen of the female changes into a broad abdomen there is much variation as to the extent of the change; and a few individuals with incomplete abdomen may still be found in older stages after the great majority have developed the complete abdomen, characteristic of full-grown females.

# SHORTER ARTICLES AND DISCUSSION

## GENES FOR THE EXTENSION OF BLACK PIGMENT IN THE CHICKEN[1]

QUITE recently Dunn[2] has reported a dominant autosomal gene which extends black pigment to all or nearly all of the plumage in chickens. This gene he has called "extension of melanic pigment," assigning the symbol $E^m$. Its recessive allelomorph ($e^m$) in the homozygous condition is present in the Light Brahma, the Columbian varieties of the several breeds which are like the Light Brahma in color and color distribution, and in the so-called red and buff varieties in which red replaces the white or silver of the Light Brahma.

Certain matings which the writer has made for the purpose of studying the hereditary behavior of other characters tend to confirm his interpretation. A White Plymouth Rock ♂ × Light Brahma ♀ gave an $F_1$ all of which showed the extension of black pigment throughout the plumage. Differences were noted between the males and females, which, as explained by Dunn, are due to a sex-linked gene which is not concerned in this discussion. With this, as with other crosses to be mentioned, the progeny frequently, indeed usually, showed the presence of genes other than those under discussion, which are incompletely hypostatic to black. In reporting self-blacks and self-blues these are disregarded.

The back crosses, $F_1$ ♀ × Light Brahma ♀, and $F_1$ ♂ × White Plymouth Rock ♀, gave only the classes expected on the basis of Dunn's interpretation. The first gave only blacks and the Columbian pattern. The second gave only blacks and whites. In both cases there was a preponderance of blacks, the ratio being, in the first case, 16 blacks to 7 Columbians, and in the second, 31 blacks to 20 whites. In each case equal numbers of the two classes reported were to be expected. The reason for these aberrant ratios is not apparent. In the $F_2$ the three expected classes appeared though there was quite a deficiency in numbers in the Columbian class. The ratio secured was 25 white, 50 black and 13 Columbian, the theoretical expectation being 22-44-22.

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[1] Contribution from the Department of Poultry Husbandry, Kansas Agricultural Experiment Station, No. 20.

[2] Dunn, L. C., 1922, AMER. NAT., 56: 464–466.

Dunn reported that he had found the gene $E^m$ in White Plymouth Rocks and the classes obtained in the crosses reported above are those expected on the assumption that the White Plymouth Rock, though lacking a dominant autosomal gene necessary for the production of melanic pigment, carries in homozygous condition the gene for its extension ($E^m$), while the Light Brahma is of the constitution $e^me^m$ and carries the dominant gene necessary for the production of black pigment, which the White Plymouth Rock lacks.

The writer[8] has reported on a gene for the extension of black pigment in the chicken involved in the hereditary behavior of blue as found in the Andalusian and other breeds. This is also an autosomal gene which has been designated as E. It is a matter of interest to ascertain whether $E^m$ and E are in reality the same gene. The Blue Splashed Andalusian ♂ × Light Brahma ♀ cross, or its reciprocal, should give evidence regarding the situation, as the Light Brahma does not carry $E^m$ and the Blue Splashed Andalusian does not carry E. Such a cross was made by the writer during the past season with the result that of twenty-three chicks hatched all proved to be self-blue.

Mated with this Blue Splashed Andalusian male at the same time were a Buff Orpington, a Rhode Island Red and a Lakenvelder female. The first two show the Columbian pattern with red replacing the white, while the latter is a white bird with black markings similar to, but not identical with, the Light Brahma, probably a modification of the Columbian pattern.

These three females gave only self-blue chicks in the numbers indicated as follows: Buff Orpington—three; Rhode Island Red—ten; and the Lakenvelder—sixteen. The chicks out of the Buff Orpington and Lakenvelder were blue in the down as well as in the adult plumage, while the chicks out of the Rhode Island Red were classified as black in the down, not becoming noticeably blue until nearly grown.

The most reasonable interpretation of these results seems to be that the Light Brahma, Buff Orpington, Rhode Island Red, and presumably the Lakenvelder, which did not carry $E^m$, did carry E, while the Blue Splashed Andalusian carried $E^m$. This indicates that two separate genes for the extension of black pigment were being dealt with. Since none of the $F_1$ generation showed the Columbian pattern, the Splashed male must have been homozygous for $E^m$.

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[8] Lippincott, W. A., 1918, Amer. Nat., 52: 95–115, and 1921, Amer. Nat., 55: 289–327.

Mated with the Blue Splashed Andalusian male at the same time were females of several other breeds all of which gave self-blue chicks only, in the numbers indicated in the following list, except as noted. The exception is reasonably explained without interfering with the probability that each of these females carried the gene E in the homozygous condition.

| Breed | No of Chicks | Color |
|---|---|---|
| Silver Spangled Hamburg | 7 | Self blue |
| White Cornish | 3 | Self blue |
| Brown Leghorn | 1 | Self blue |
| Silver Wyandotte | 4 | Self blue |
| White Langshan | 9 | Self blue |
| White Silky | 4 | Self blue |
| White Minorca | 14 | 5 self blue<br>9 white (blue spots) |

The exception to the production of all self-blue chicks came from the White Minorca. This bird was evidently heterozygous for a gene for dominant white. The slight spotting or flecking noted in the white chicks was typical of heterozygous dominant whites and not at all to be confused with blue splashed. The pigmented spots were in every case blue, as was to be expected.

In a former paper[4] evidence was presented indicating that the gene E was carried by White Plymouth Rocks, White Wyandottes and Black Langshans and its presence in White Leghorns was reported as probable. Further matings have shown unmistakably that this gene may be carried by White Leghorns in which the white (assigned the symbol I by Hadley[5]) is dominant. The $F_2$ generation from a Blue Splashed Andalusian ♂ × White Leghorn ♀ cross contains among other classes self-blues and self-blacks (disregarding the influence of the sex-linked gene for barring carried by the White Leghorn as shown by Hadley[6]), which can be explained only on the assumption that the White Leghorn carried the gene E.

There is evidence, therefore, that this gene (E) is rather widely distributed among breeds of chickens and may be carried by individuals of the White Plymouth Rock; White, and Silver Wyandotte; Black, and White Langshan; Black, White, and Buff Orpington; Light Brahma; Lakenvelder; Silver Spangled Hamburg; White Cornish; Brown, and White Leghorn; White Silky; and White Minorca breeds. It has in fact given no evidence of being in other than the homozygous condition in any individual of these several breeds, which has been mated and which has produced chicks, except certain ones noted in a previous paper[7] that proved to carry R, a gene cooperating with E to produce self-blue and which is either allelomorphic to E, or so closely linked to its recessive allelomorph that it has not been separated experimentally.

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[4] Lippincott, W. A., 1921, AMER. NAT., 55: 289–327.

[5] Hadley, P. B., 1913, Rhode Island Agr. Exp. Sta. Bulletin 155: 151–216.

[6] *Loc. cit.*

There are several genes found in chickens which result in the inhibition of black pigment in certain parts of feathers or regions of the plumage, resulting in the appearance of a more or less definite color pattern. The possibility that the allelomorphs of such genes, whose somatic expression is alternative to self-black, may be necessary to complete the chain of developments and reactions which result in the extension of black pigment to all parts of the plumage even though they are recessive, should not be overlooked. If such a view is ultimately proved tenable, there are not two only, but several genes for the extension of black pigment in the chicken.

WILLIAM A. LIPPINCOTT

KANSAS AGRICULTURAL EXPERIMENT STATION

[7] Lippincott, W. A., 1919, *Jour. Heredity*, 10: 7–79.

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# EXPERIMENTAL STUDIES ON THE DURATION OF LIFE

## VIII. THE INFLUENCE UPON DURATION OF LIFE OF CERTAIN MUTANT GENES OF DROSOPHILA MELANOGASTER[1]

BIENVENIDO MARIA GONZALEZ

### INTRODUCTION

IN the first part of this series Pearl and Parker (27) showed that there was a marked difference in the duration of life and in the form of the $l_x$ curve in wild type stocks of *Drosophila* and a synthetic quintuple mutation stock. It was also pointed out in a general way that this difference was hereditary and Mendelian.

Previous to t[illegible]work of Pearl and Parker (27, 32, 44, 49, 50, 61) th[illegible]ve been a few other studies on the duration of li[illegible]*rosophila*. In 1911 Moenkhaus (10) made a casua[illegible]nce to the fact that female flies were kept alive 15[illegible] In 1913 Hyde (11) in studying fertility and ste[illegible]d two strains of *Drosophila* which differed greatly [illegible] their duration of life. On breeding these he found evidence that the $F_1$ flies were longer lived than either parent race, and also found some indications that there was a segregation of long and short lived flies in the second filial generation ($F_2$). Loeb and Northrop

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[1] Papers from the Department of Biometry and Vital Statistics, School of Hygiene and Public Health, Johns Hopkins University. No. 87.

Since this investigation by Dr. Gonzalez was planned and carried out as a part of the general study of duration of life going forward in this laboratory, it was thought proper to publish it in the present series. It should be said, however, that while this study forms an integral part of the work of the laboratory, Dr. Gonzalez is entirely responsible for the results and conclusions reached. Raymond Pearl.

(14–16), Northrop (17) and Lutz (13) made a number of experiments on the effects of food and temperature on the duration of life of *Drosophila.* All this early work is adequately reviewed by Pearl and Parker (*loc. cit*).

From the above papers, and the facts gathered together by Pearl (52) from the general field of biology, there seems to be little room for doubt as to the inheritance of duration of life. This fact being established, the next obvious step is to study what the factors are that control the inheritance of this character. We do know from the work of Morgan (9) and others, of numerous physical characters of an individual directly traceable to the active units of the nucleus of a cell—the chromosomes, and we know something of the behavior of these chromosomes, and the genes that are borne in them, in inheritance. But what bearing do the genes have on duration of life? Pearl, Parker and Gonzalez (57) have lately shown in great detail that in *Drosophila* duration of life is inherited in a strictly Mendelian manner. They, however, paid attention to but one m[illegible]phological mutation, namely, vestigial. It is the pur[illegible] of the present paper to inquire in more detail into [illegible]luence of each of several known and established m[illegible]s upon duration of life.

## MATERIAL AND ME[illegible]

The stocks used were the Old Falmouth (wild) and the synthetic stock containing five mutants obtained from Morgan's laboratory. For convenience, the description of these two stocks as given in the first paper of Pearl and Parker is herewith reproduced:

1. **Old Falmouth, Wild type fly, long bred in Morgan's laboratory. More inbred than 2 (New Falmouth).**
4. **Quintuple. A synthetic stock, carrying five second chromosome mutations, each in homozygous form, as follows: black, purple, vestigial, arc, and speck. Other characters wild type (Morgan). A brief description of these mutations is as follows:**
   **Black is a color factor affecting the body and the extremities.**
   **Purple is an eye color factor of the hue indicated by its name.**
   **Vestigial is a wing mutation in which the flies have tiny scales**

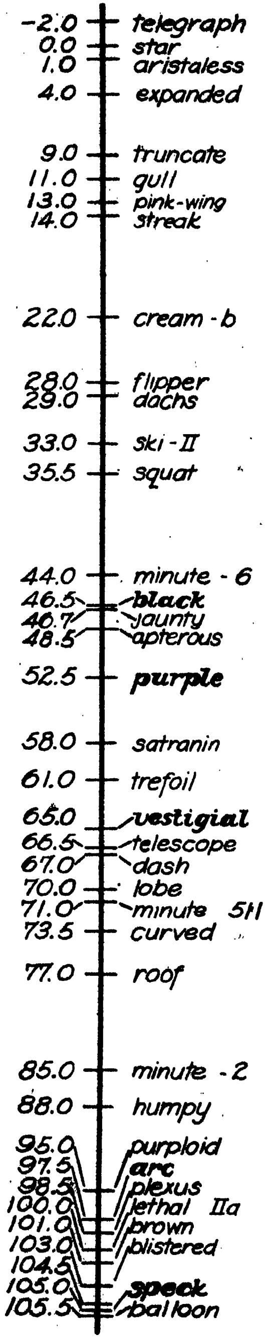

FIG. 1. Map showing the distribution of mutant loci in the second chromosome of *Drosophila melanogaster* (Oct. 15, 1920). The five mutants involved in this study are in heavier lettering.

in place of wings. The "balancers" (halteres) are similarly modified, though not to the same degree as the wings.

Arc is a wing mutation in which the wings are bent downward in an even curve, presenting a convex surface.

Speck has reference to a minute and intensely black spot in the axil of each wing.

A more detailed account and description of the above mutants may be found in Bridges and Morgan (58).

The latest map of the second chromosome as given by Bridges (59) is reproduced in Fig. 1 with the mutations used in the present study in heavier lettering.

The technique was in general the same as that described by Pearl and Parker (27). Individual matings were made with flies half a day old or younger and placed in half-pint milk bottles provided with banana agar medium. On the sixth or seventh day the parents were transferred to a second half-pint bottle. The progeny from these bottles for nine days, counting from the first day on which hatches were observed, were emptied into one ounce vials containing banana agar and these were kept separate and labeled as born on that day, and their duration of life observed. After nine days hatching the half-pint bottles were discarded. The parents have been transferred in the meanwhile into vials for observation of their duration of life also. The bottles were examined for dead flies every day, and they were changed three times during the week to give the flies fresh food. The method of handling the records was the same as that described in Pearl and Parker (27) and need not be repeated here. All these flies were kept at a constant temperature of 25° C. in an electric incubator.

Reciprocal crosses of the wild and quintuple stock were made and the $F_1$'s mated. Cross-overs were observed and as many combinations as possible were obtained and purified. These new combinations were labeled according to their mutant phenotypic characters as follows:

| | | |
|---|---|---|
| 00 | b | (Black) |
| 01 | pr | (Purple) |
| 02 | vg | (Vestigial) |
| 03 | a | (Arc) |
| 04 | sp | (Speck) |

| | |
|---|---|
| 10 | bpr |
| 11 | b vg |
| 12 | b a |
| 13 | b sp |
| 14 | prvg |
| 15 | pr a |
| 16 | pr sp |
| 17 | asp |
| 20 | bpr vg |
| 21 | bpr a |
| 22 | bpr sp |
| 23 | b asp |
| 24 | pr asp |
| 25 | vg asp |
| 30 | bpr asp |
| 31 | b vgasp |
| 32 | prvgasp |

The above, together with the original stocks, make a total of twenty-four different combinations of mutant genes.

Inasmuch as the character Arc is shielded when in combination with Vestigial, all Vestigial stocks were tested for the presence of Arc towards the end of the experiment. They were mated with a stock pure for Arc and containing no other mutant, and therefore dominant for Vestigial. All stocks containing Arc should give 100 per cent. Arc progeny if they are pure for this character; *vice versa,* they should show 100 per cent. straight wing (dominant to Arc) if they are pure for the absence of the character Arc. An intermediate condition shows impurity as far as the character Arc or its dominant allelomorph is concerned. Three males and three females from each bottle where progeny were obtained for the duration of life experiments were thus tested. The test revealed the following:

TABLE I

TEST OF VESTIGIAL STOCKS FOR ARC

| No. | Original Designation | Result of Test | New Designation |
|---|---|---|---|
| 02 | vg | No Arc | same |
| 11 | b vg | No Arc | same |
| 14 | prvg | No Arc | same |
| 20 | bprvg | Not pure | bprvga/ |
| 25 | vgasp | Pure for Arc | same |
| 31 | b vgasp | Not pure | b vga/sp |
| 32 | prvg asp | No Arc | prvg sp |
| | Quintuple bprvgasp | Pure for Arc | same |

This work was carried out under the direction of Dr. Raymond Pearl, from whom I received most valuable advice and encouragement. Miss Sylvia L. Parker was a constant counsellor in the details of the experimental work. Without the help of Mr. James Krucky in the preparation of media, this work could not have proceeded with the rapidity that it has. I also wish to express my indebtedness to Misses Beryl L. Reed and Mary Connor for punching my records on cards for mechanical tabulation.

## FERTILITY

It was the plan to raise at least 500 individuals of each strain. For this purpose as many matings were started as were necessary to produce at least 500 flies for the duration of life experiments. Table II. shows the strains, the number of matings, the total progeny and the average progeny for nine days for the fertile matings.

TABLE II

MATINGS

| Strain | No. of Fertile Matings | Progeny | | | Per cent Males | Average Progeny per Fertile Mating |
|---|---|---|---|---|---|---|
| | | ♂ | ♀ | Total | | |
| Wild | 5 | 560 | 676 | 1236 | 45 | 247 |
| Quintuple | 18 | 365 | 420 | 785 | 46 | 44 |
| b | 5 | 335 | 355 | 690 | 49 | 138 |
| pr | 6 | 944 | 1006 | 1950 | 48 | 325 |
| vg | 10 | 245 | 288 | 533 | 46 | 53 |
| a | 7 | 417 | 470 | 887 | 47 | 127 |
| sp | 6 | 301 | 318 | 619 | 49 | 103 |
| bpr | 6 | 697 | 787 | 1484 | 47 | 247 |
| b vg | 5 | 307 | 388 | 695 | 44 | 139 |
| b a | 6 | 428 | 466 | 894 | 48 | 149 |
| b sp | 16 | 528 | 601 | 1129 | 47 | 71 |
| prvg | 10 | 568 | 523 | 1091 | 52 | 109 |
| pr a | 5 | 497 | 652 | 1149 | 43 | 230 |
| pr sp | 13 | 1465 | 1750 | 3215 | 46 | 247 |
| asp | 6 | 315 | 321 | 636 | 50 | 106 |
| bprvga/ | 9 | 600 | 616 | 1216 | 49 | 135 |
| bpr a | 5 | 413 | 574 | 987 | 42 | 197 |
| bpr sp | 27 | 432 | 624 | 1056 | 41 | 39 |
| b asp | 17 | 312 | 270 | 582 | 54 | 34 |
| pr asp | 6 | 331 | 376 | 707 | 47 | 118 |
| vgasp | 8 | 287 | 279 | 566 | 51 | 71 |
| bpr asp | 26 | 400 | 576 | 976 | 41 | 38 |
| b vga/sp | 16 | 320 | 306 | 626 | 51 | 39 |
| prvg sp | 5 | 276 | 302 | 578 | 48 | 116 |
| Totals | 243 | 11343 | 12944 | 24287 | | |

The preceding table shows at a glance the wide variability in fertility of the different strains.

The fertility value of each mutant gene, using strains containing one and two mutations[2] only, is shown in Table III.

TABLE III

FERTILITY VALUE OF MUTANTS

| Strains | Total Average Progeny of Strains | Average Progeny per Strain |
|---|---|---|
| b, bpr, b vg, b a, b sp | 744 | 149 |
| pr, bpr, prvg, pr a, pr sp | 1158 | 232 |
| vg, b vg, prvg, | 301 | 100 |
| a, b a, pr a, asp | 612 | 153 |
| sp, b sp, pr sp, asp | 527 | 132 |

Examination of the table discloses the fact that the strains having high fertility usually have purple, and those of low values almost invariably contain Vestigial. There is here a suggestion of the presence of a gene or genes determining fertility closely linked to one or more of the mutant genes studied.[3] It is hoped that at some future time a further study of this character may be made.

## DURATION OF LIFE OF STRAINS CARRYING ONE MUTATION ONLY

Table IV gives the survivorship data of the five pure mutants and the original stocks.

Fig. 2 shows graphically the course taken by the $l_x$ lines when plotted on an arithlog grid. It may be observed that neither Black nor Speck gives a survivorship curve much different from the wild parent. Purple and Arc are considerably lower than the wild stock but higher than the Quintuple. The life curve of Vestigial is the one closest to the Quintuple, though not quite as low as that.

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[2] Strains involving more than two mutations would tend to mask each other's effects to a degree that would render their grouping valueless.

[3] It is at least equally probable that the true explanation of these differences in fertility associated with the presence of certain morphological mutations is the same as that for similar association of definite degrees of duration of life, set forth by Pearl, Parker and Gonzalez (57), and adopted by Gonzalez himself in the present paper *infra*.—R. P.

TABLE IV

Survivorship Distribution of Original Stocks and Single Mutants (Both sexes included, not weighted)

| Age in Days | Number of Survivors up to Indicated Age | | | | | | |
|---|---|---|---|---|---|---|---|
| | Wild | Quintuple | Black | Purple | Vestigial | Arc | Speck |
| 1 | 1000 | 1000 | 1000 | 1000 | 1000 | 1000 | 1000 |
| 4 | 998 | 955 | 991 | 995 | 996 | 986 | 985 |
| 7 | 992 | 683 | 987 | 939 | 938 | 938 | 977 |
| 10 | 971 | 424 | 974 | 873 | 809 | 873 | 963 |
| 13 | 948 | 269 | 970 | 791 | 664 | 813 | 932 |
| 16 | 901 | 168 | 949 | 711 | 527 | 760 | 900 |
| 19 | 882 | 115 | 928 | 622 | 394 | 709 | 884 |
| 22 | 858 | 75 | 890 | 558 | 306 | 643 | 855 |
| 25 | 831 | 48 | 854 | 495 | 206 | 575 | 827 |
| 28 | 799 | 31 | 832 | 425 | 150 | 464 | 792 |
| 31 | 743 | 13 | 768 | 338 | 105 | 402 | 745 |
| 34 | 705 | 6 | 690 | 218 | 62 | 316 | 687 |
| 37 | 592 | 5 | 619 | 151 | 43 | 241 | 643 |
| 40 | 519 | 1 | 503 | 99 | 30 | 165 | 614 |
| 43 | 424 | 0 | 420 | 67 | 8 | 107 | 544 |
| 46 | 342 | — | 371 | 34 | 2 | 62 | 468 |
| 49 | 247 | — | 293 | 20 | 0 | 32 | 417 |
| 52 | 194 | — | 241 | 7 | — | 15 | 333 |
| 55 | 117 | — | 196 | 3 | — | 2 | 273 |
| 58 | 88 | — | 119 | 1 | — | 1 | 207 |
| 61 | 67 | — | 65 | 0 | — | 1 | 149 |
| 64 | 45 | — | 30 | — | — | 0 | 102 |
| 67 | 32 | — | 20 | — | — | — | 50 |
| 70 | 20 | — | 14 | — | — | — | 24 |
| 73 | 8 | — | 3 | — | — | — | 15 |
| 76 | 1 | — | 1 | — | — | — | 2 |
| 79 | 0 | — | 0 | — | — | — | 2 |
| 82 | — | — | — | — | — | — | 0 |
| Abs. No. of flies | 1236 | 785 | 690 | 1950 | 533 | 887 | 619 |

Inasmuch as these mutations affect the duration of life of the two sexes differently, it is interesting to note just what are the differences in the various strains and how such variations are affected by the combination of two or more mutants in a single individual. The data in Table VI are derived from Table V.

In Black there is no significant difference in the mean duration of life of males and females, while there is in case of all other mutations. Combining Black with any of the other mutations does not alter the difference between the sexes in duration of life. In the case of Black-speck there is less difference between the duration of life of the males and females than in the case of Speck, seeming to imply that Black, while having no effect when alone or with Purple, Vestigial or Arc, does have the effect of reducing the sex difference in Speck. This effect of Black on Speck is consistent throughout, as will be noticed later on.

Purple-speck shows no significant difference in the duration of life of males and females. Purple with Vestigial gives about the same result as Vestigial alone, indicating that Vestigial overshadows any effects of Purple in so far as the character in question is concerned. In Purple-arc the effect of Purple is the dominant one.

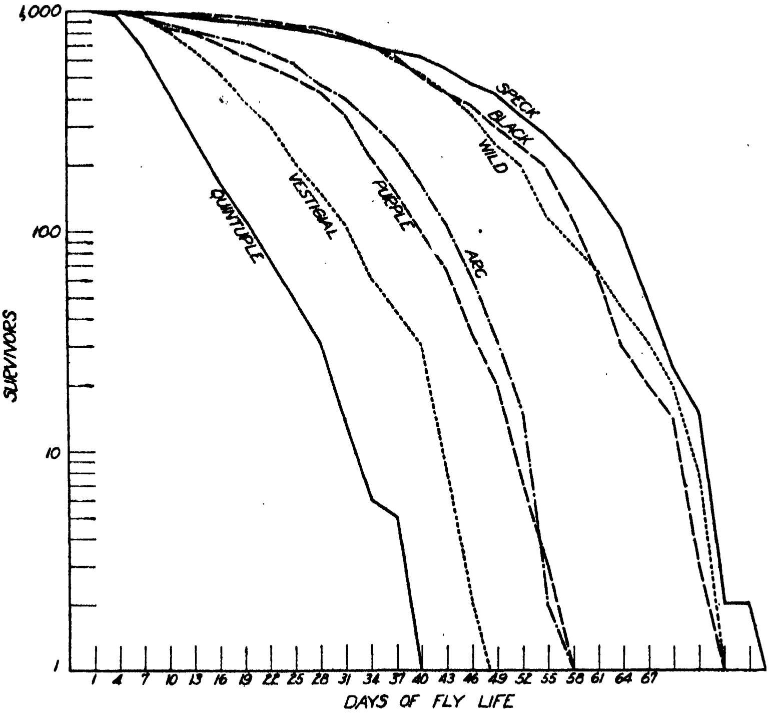

FIG. 2. Survivorship graphs of original stocks and single mutants. Both sexes.

In Arc-speck the result is almost the algebraic sum of the two single mutations. The greater mean duration of life is in the same direction as Speck, which has the greater value.

If we continue our observations along the same line on the other combinations involving more than two mutants, the results are not materially different from those noted above. They are further complicated by interactions among themselves, however. For example: compare Black-purple-vestigial, not pure for Arc (♂ < ♀ 7.39), with Purple-vestigial (♂ < ♀ 7.33); Black-purple-arc (♀ < ♂ 4.50) with Purple-arc (♀ < ♂ 4.02); Black-arc-speck (♀ < ♂ 6.77) with Arc-speck (♀ < ♂ 3.72), etc.

Other instances of the evidence of the effect of single characters when all others are common to both strains in question are: Vestigial-arc-speck (♂ < ♀ 12.39) compared with Arc-speck (♀ < ♂ 3.72), Vestigial being (♂ < ♀ 6.00); Black-purple-arc-speck (♂ < ♀ .46) with Vestigial-black-purple-arc-speck (♂ < ♀ 2.67).

In other cases when the mutants involved have specific interactions among themselves, the results are not as regular. Compare Black-purple-speck (♀ < ♂ 6.77) with

TABLE V

DURATION OF LIFE OF DIFFERENT STRAINS

| Strains | Mean Duration of Life | | | Differences between males and females ♂—♀ | Difference ÷ P. E. of Diff. |
|---|---|---|---|---|---|
| | Both sexes (actual number) | Males | Females | | |
| Wild | 39.47±.28 | 38.08±.36 | 40.62±.42 | — 2.54±.55 | 4.62 |
| Quintuple | 10.88±.16 | 9.45±.17 | 12.12±.25 | — 2.07±.30 | 8.90 |
| Black | 40.68±.50 | 41.03±.53 | 40.33±.51 | + 0.70±.74 | .95 |
| Purple | 24.54±.18 | 27.42±.27 | 21.83±.23 | + 5.59±.35 | 15.97 |
| Vestigial | 18.22±.29 | 14.98±.28 | 20.98±.40 | — 6.00±.49 | 12.24 |
| Arc | 26.81±.29 | 25.20±.33 | 28.24±.37 | — 3.04±.50 | 6.08 |
| Speck | 42.66±.47 | 46.63±.63 | 38.91±.65 | + 7.72±.91 | 8.48 |
| bpr | 27.35±.24 | 30.44±.34 | 24.06±.32 | + 6.38±.47 | 13.57 |
| b vg | 20.78±.25 | 16.45±.23 | 24.20±.40 | — 7.75±.46 | 16.85 |
| b a | 21.71±.26 | 20.11±.36 | 23.17±.37 | — 3.06±.52 | 5.88 |
| b sp | 31.09±.24 | 32.36. ±35 | 29.97±.31 | + 2.39±.47 | 5.09 |
| prvg | 15.43±.15 | 11.72±.13 | 19.05±.27 | — 7.33±.30 | 24.43 |
| pr a | 33.71±.34 | 36.00±.53 | 31.98±.43 | + 4.02±.68 | 5.91 |
| pr sp | 23.30±.14 | 23.72±.22 | 22.96±.19 | + 0.76±.29 | 2.62 |
| asp | 36.53±.44 | 38.41±.58 | 34.69±.66 | + 3.72±.88 | 4.23 |
| bpr a | 32.50±.34 | 35.06±.55 | 30.56±.42 | + 4.50±.69 | 6.52 |
| bpr sp | 27.25±.29 | 31.22±.45 | 24.45±.37 | + 6.77±.58 | 11.67 |
| b asp | 30.50±.39 | 33.72±.53 | 26.80±.53 | + 6.92±.75 | 9.22 |
| pr asp | 39.64±.45 | 38.38±.62 | 40.67±.45 | — 2.29±.77 | 2.97 |
| vgasp | 18.97±.37 | 12.81±.26 | 25.20±.61 | —12.39±.66 | 18.77 |
| prvg sp | 10.62±.16 | 9.47±.17 | 12.17±.26 | — 2.70±.31 | 8.71 |
| bprvga/ | 18.53±.18 | 14.79±.16 | 22.18±.29 | — 7.39±.33 | 22.39 |
| b vga/sp | 16.70±.25 | 13.97±.26 | 19.56±.41 | — 5.59±.49 | 11.40 |
| bpr asp | 22.92±.28 | 22.65±.42 | 23.11±.38 | — 0.46±.57 | .81 |

TABLE VI

A COMPARISON OF THE MEAN DURATION OF LIFE OF THE TWO SEXES

| Stocks | Excess in Mean Duration of Life in Days | |
|---|---|---|
| | Males live longer than females | Females live longer than males |
| Black | .70±.74 | |
| Purple | 5.59±.35 | |
| Speck | 7.72±.91 | |
| Vestigial | | 6.00±.49 |
| Arc | | 3.04±.50 |
| Black-purple | 6.38±.47 | |
| Black-speck | 2.39±.47 | |
| Black-vestigial | | 7.75±.46 |
| Black-arc | | 3.06±.52 |
| Purple-speck | 0.76±.29 | |
| Purple-arc | 4.02±.68 | |
| Purple-vestigial | | 7.33±.30 |
| Arc-speck | 3.72±.88 | |
| Black-purple speck | 6.77±.58 | |
| Black-purple-arc | 4.50±.69 | |
| Black-purple-vestigial-arc/ | | 7.39±.33 |
| Black-arc-speck | 6.92±.75 | |
| Purple arc-speck | | 2.29±.77 |
| Vestigial-arc-speck | | 12.39±.66 |
| Purple-vestigial-speck | | 2.70±.31 |
| Black-purple-arc-speck | | .46±.57 |
| Black-vestigial-arc /speck | | 5.59±.49 |
| Black-purple-vestigial-arc-speck | | 2.67±.30 |

Purple-speck (♀ < ♂ 0.76). We have noted before this the irregular behavior of Speck combinations with either Black or Purple.

This instance of a character having a different expression in the two sexes, without involving necessarily any difference in the sex chromosomes, is not at all new. Bridges and Morgan (58) and Lynch (60). give an account of differential fertility in various mutant stocks of *Drosophila*. The females of "rudimentary" and "fused" wings in the first chromosome, "morula" and "reduced bristle" in the second, and "dwarf" in the third are infertile, while the males are fully fertile. The case is reversed in "cleft" wings of the first chromosome where the males are fertile and the females infertile.

Cases of differential fertility are by no means the rule in the first chromosome, and such instances as have been noted above can only be conceived as being effects of the mutant genes *per se*. Then of course we have the general phenomenon of no crossing-over in the male.

Two other cases of sexual differences in the expression of a character where genes are in autosomal chromosomes have come to the notice of the writer. As these data are as yet unpublished no further mention can be made here. All we are interested in showing at present is that these sex differences in duration of life have a parallel in the literature of *Drosophila*. The basic cause of these differences may or may not be the same.

## Inheritance of Duration of Life in Males

Since sex does not affect duration of life uniformly in one direction in the different strains involved in these

TABLE VII

Survivorship Distribution of Males of Original Stocks and Strains Involving Single Mutations

| Age in Days | Number of Survivors up to Indicated Age | | | | | | |
|---|---|---|---|---|---|---|---|
| | Wild | Quintuple | Black | Purple | Vestigial | Arc | Speck |
| 1 | 1000 | 1000 | 1000 | 1000 | 1000 | 1000 | 1000 |
| 4 | 998 | 953 | 994 | 994 | 1000 | 990 | 990 |
| 7 | 998 | 655 | 991 | 958 | 922 | 921 | 987 |
| 10 | 984 | 356 | 976 | 904 | 727 | 837 | 980 |
| 13 | 968 | 173 | 976 | 836 | 563 | 751 | 960 |
| 16 | 937 | 85 | 961 | 771 | 384 | 688 | 934 |
| 19 | 912 | 44 | 943 | 706 | 273 | 628 | 924 |
| 22 | 879 | 22 | 896 | 654 | 184 | 573 | 897 |
| 25 | 854 | 19 | 863 | 602 | 73 | 516 | 877 |
| 28 | 821 | 11 | 839 | 537 | 24 | 393 | 854 |
| 31 | 757 | 0 | 764 | 448 | 8 | 343 | 824 |
| 34 | 716 | — | 678 | 302 | 0 | 283 | 784 |
| 37 | 541 | — | 606 | 222 | — | 230 | 751 |
| 40 | 429 | — | 504 | 155 | — | 165 | 728 |
| 43 | 327 | — | 427 | 107 | — | 118 | 651 |
| 46 | 223 | — | 367 | 59 | — | 79 | 571 |
| 49 | 129 | — | 290 | 37 | — | 36 | 525 |
| 52 | 105 | — | 248 | 13 | — | 17 | 415 |
| 55 | 71 | — | 218 | 4 | — | 0 | 332 |
| 58 | 59 | — | 131 | 1 | — | — | 262 |
| 61 | 50 | — | 78 | 0 | — | — | 196 |
| 64 | 39 | — | 45 | — | — | — | 136 |
| 67 | 29 | — | 27 | — | — | — | 76 |
| 70 | 20 | — | 24 | — | — | — | 37 |
| 73 | 12 | — | 3 | — | — | — | 20 |
| 76 | 2 | — | 3 | — | — | — | 0 |
| 79 | 0 | — | 0 | — | — | — | — |
| Abs. No. of flies | 560 | 365 | 335 | 944 | 245 | 417 | 301 |

studies, it is deemed advisable to study the two sexes separately and thus eliminate an item which will obviously complicate the interpretation of results and mask or accentuate differences through its alternating differential effect.

Table VII gives the survivorship distributions of males of the parent stocks and the five pure mutants.* These figures are not very different from those in Table IV which give the survivorship distributions for whole populations. Due to the differential effect of sex the relative position of Arc and Purple are reversed. These two characters, however, have about the same duration of life and this difference is not important. Fig. 3 shows the data in Table VII graphically. The survivorship data for the different combinations are given in Tables VIII and IX.

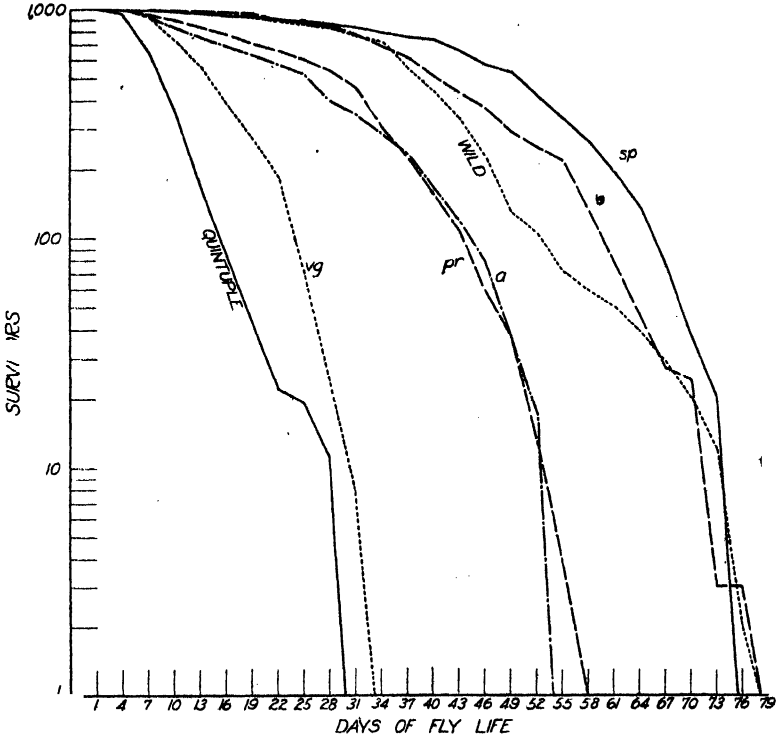

FIG. 3. Survivorship graphs of original stocks and single mutants. Males.

TABLE VIII

SURVIVORSHIP DISTRIBUTION OF MALES OF STRAINS INVOLVING TWO MUTATIONS

| Age in Days | Number of Survivors up to Indicated Age | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | bpr | b vg | b a | b sp | prvg | pr a | pr sp | asp |
| 1 | 1000 | 1000 | 1000 | 1000 | 1000 | 1000 | 1000 | 1000 |
| 4 | 997 | 993 | 986 | 996 | 972 | 992 | 973 | 994 |
| 7 | 971 | 974 | 907 | 983 | 901 | 978 | 924 | 984 |
| 10 | 924 | 876 | 825 | 962 | 611 | 944 | 832 | 968 |
| 13 | 887 | 707 | 724 | 949 | 336 | 915 | 745 | 949 |
| 16 | 832 | 472 | 565 | 922 | 146 | 871 | 691 | 911 |
| 19 | 768 | 280 | 463 | 864 | 67 | 813 | 623 | 879 |
| 22 | 717 | 163 | 355 | 763 | 28 | 748 | 554 | 822 |
| 25 | 656 | 94 | 276 | 687 | 11 | 666 | 463 | 784 |
| 28 | 582 | 55 | 227 | 617 | 2 | 610 | 364 | 746 |
| 31 | 492 | 26 | 180 | 532 | 0 | 545 | 282 | 686 |
| 34 | 418 | 7 | 136 | 470 | — | 485 | 205 | 600 |
| 37 | 336 | 3 | 100 | 379 | — | 457 | 151 | 537 |
| 40 | 264 | 0 | 68 | 282 | — | 412 | 100 | 495 |
| 43 | 184 | — | 30 | 201 | — | 384 | 61 | 441 |
| 46 | 131 | — | 14 | 159 | — | 338 | 34 | 371 |
| 49 | 75 | — | 12 | 87 | — | 292 | 24 | 289 |
| 52 | 44 | — | 5 | 61 | — | 217 | 15 | 216 |
| 55 | 19 | — | 2 | 27 | — | 169 | 12 | 127 |
| 58 | 9 | — | 0 | 8 | — | 135 | 9 | 67 |
| 61 | 6 | — | — | 4 | — | 97 | 4 | 48 |
| 64 | 3 | — | — | 2 | — | 64 | 3 | 29 |
| 67 | 1 | — | — | 0 | — | 33 | 2 | 13 |
| 70 | 0 | — | — | — | — | 0 | 1 | 3 |
| 73 | — | — | — | — | — | — | 1 | 3 |
| 76 | — | — | — | — | — | — | 0 | 3 |
| 79 | — | — | — | — | — | — | — | 3 |
| 82 | — | — | — | — | — | — | — | 3 |
| 85 | — | — | — | — | — | — | — | 0 |
| Abs. No. of flies | 697 | 307 | 428 | 528 | 568 | 497 | 1465 | 315 |

Examining Table X (biometric constants) we find that the mean duration of life of Black of 41.03 ± .53 days and that of Speck of 46.63 ± .63 are higher than that of the Wild stock, which is only 38.08 days. The difference between Wild and Black of 2.95 ± .64 days is not large although significant, but that between Wild and Speck, 8.55 ± .72, is very large. There is a suggestion in this of the presence of a mutant factor that increases the duration of life. Fig. 3 shows this rather clearly. Purple and Arc give a lower duration of life than the Wild stock, and Vestigial still lower.

Since we have data for so many combinations, the results are difficult to interpret *en masse*. Close observa-

## TABLE IX

### SURVIVORSHIP DISTRIBUTION OF MALES OF STRAINS INVOLVING THREE AND FOUR MUTATIONS

| Age in Days | Number of Survivors up to Indicated Age | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | bpr a | bpr sp | b asp | pr asp | vgasp | prvg sp | bpr vga/ | b vga/sp | bpr asp |
| 1 | 1000 | 1000 | 1000 | 1000 | 1000 | 1000 | 1000 | 1000 | 1000 |
| 4 | 995 | 988 | 990 | 997 | 990 | 978 | 995 | 972 | 975 |
| 7 | 978 | 956 | 974 | 979 | 864 | 659 | 940 | 881 | 925 |
| 10 | 947 | 924 | 939 | 949 | 617 | 315 | 800 | 672 | 830 |
| 13 | 896 | 866 | 904 | 918 | 362 | 123 | 595 | 456 | 753 |
| 16 | 852 | 819 | 865 | 888 | 206 | 18 | 353 | 313 | 655 |
| 19 | 804 | 764 | 843 | 849 | 167 | 11 | 202 | 194 | 573 |
| 22 | 760 | 722 | 798 | 834 | 111 | 7 | 95 | 153 | 470 |
| 25 | 695 | 678 | 737 | 795 | 56 | 7 | 52 | 97 | 370 |
| 28 | 646 | 627 | 625 | 731 | 28 | 4 | 32 | 59 | 295 |
| 31 | 569 | 556 | 577 | 665 | 17 | 4 | 22 | 22 | 230 |
| 34 | 496 | 479 | 513 | 556 | 7 | 4 | 7 | 6 | 187 |
| 37 | 448 | 389 | 458 | 502 | 3 | 4 | 3 | 0 | 150 |
| 40 | 375 | 315 | 388 | 459 | 3 | 4 | 2 | — | 117 |
| 43 | 320 | 201 | 301 | 420 | 3 | 4 | 0 | — | 73 |
| 46 | 276 | 134 | 224 | 344 | 0 | 0 | — | — | 50 |
| 49 | 240 | 86 | 160 | 299 | — | — | — | — | 27 |
| 52 | 194 | 51 | 74 | 236 | — | — | — | — | 13 |
| 55 | 123 | 21 | 22 | 184 | — | — | — | — | 10 |
| 58 | 92 | 9 | 13 | 136 | — | — | — | — | 7 |
| 61 | 75 | 5 | 0 | 100 | — | — | — | — | 5 |
| 64 | 31 | 2 | — | 66 | — | — | — | — | 0 |
| 67 | 29 | 2 | — | 42 | — | — | — | — | — |
| 70 | 10 | 0 | — | 9 | — | — | — | — | — |
| 73 | 0 | — | — | 3 | — | — | — | — | — |
| 76 | — | — | — | 0 | — | — | — | — | — |
| Abs. No of flies | 413 | 432 | 312 | 331 | 287 | 276 | 600 | 320 | 400 |

tion has revealed an order which we now propose to test out. Let us assume for the moment that each of the five mutant genes studied has a definite duration of life peculiar to it, in the same manner as other genes of *Drosophila* known to control externally visible characters are, by common observation, conceded to produce flies of low or good vitality, poor in fertility or fully fertile, etc. There is the other possibility of taking duration of life as a separate character represented by a gene or genes in the chromosome, closely linked to some or all of the characters studied. As the discussion that follows will not be affected one way or the other whichever of the two views is taken, we may leave this for the present an open question.

We will first test the reaction of the different mutants with one another in respect of duration of life.

TABLE X

BIOMETRIC CONSTANTS FOR DURATION OF LIFE OF DIFFERENT STRAINS OF MALE DROSOPHILA

| Strains | Number of flies | Mean (in days) | Standard Deviation (in days) | Coefficient of Variation |
|---|---|---|---|---|
| Wild | 560 | 38.08±.36 | 12.74±.26 | 33.46± .75 |
| bprvgasp Quintuple | 365 | 9.45±.17 | 4.75±.12 | 50.26±1.63 |
| b | 335 | 41.03±.53 | 14.35±.37 | 34.99±1.02 |
| pr | 944 | 27.42±.27 | 12.28±.19 | 44.79± .82 |
| vg | 245 | 14.98±.28 | 6.41±.20 | 42.80±1.52 |
| a | 417 | 25.20±.33 | 9.87±.23 | 39.17±1.05 |
| sp | 301 | 46.63±.63 | 16.21±.45 | 34.76±1.06 |
| bpr | 697 | 30.44±.34 | 13.19±.24 | 43.32± .92 |
| b vg | 307 | 16.45±.23 | 6.09±.17 | 37.02±1.14 |
| b a | 428 | 20.11±.36 | 10.93±.25 | 54.34±1.58 |
| b sp | 528 | 32.36±.35 | 12.09±.25 | 37.35± .88 |
| prvg | 568 | 11.72±.13 | 4.49±.09 | 38.31± .87 |
| pr a | 497 | 36.00±.53 | 17.42±.37 | 48.40±1.25 |
| pr sp | 1465 | 23.72±.22 | 12.45±.16 | 52.48± .81 |
| asp | 315 | 38.41±.58 | 15.15±.41 | 39.44±1.21 |
| bpr a | 413 | 35.06±.55 | 16.43±.39 | 46.86±1.32 |
| bpr sp | 432 | 31.22±.45 | 13.73±.32 | 43.97±1.19 |
| b asp | 312 | 33.72±.53 | 13.75±.37 | 40.78±1.27 |
| pr asp | 331 | 38.38±.62 | 16.63±.44 | 43.32±1.33 |
| vgasp | 287 | 12.81±.26 | 6.43±.18 | 50.17±1.73 |
| prvg sp | 276 | 9.47±.17 | 4.30±.12 | 45.39±1.55 |
| bprvga/ | 600 | 14.79±.16 | 5.86±.11 | 39.61± .88 |
| b vga/sp | 320 | 13.97±.26 | 7.02±.19 | 50.26±1.66 |
| bpr asp | 400 | 22.65±.42 | 12.42±.30 | 54.84±1.49 |

Combining Black with each of the others we have:

TABLE XI

| Strain | Mean Duration of Life | Strain | Mean Duration of Life | Differences |
|---|---|---|---|---|
| Black | 41.02±.53 | | | |
| Purple | 27.42±.27 | Black-purple | 30.44±.34 | + 3.02±.43 |
| Vestigial | 14.98±.28 | Black-vestigial | 16.45±.23 | + 1.47±.36 |
| Arc | 25.20±.33 | Black-arc | 20.11±.36 | — 5.09±.49 |
| Speck | 43.63±.63 | Black-speck | 32.36±.35 | —14.27±.72 |

From the above we can see that Black raises the value of Purple and Vestigial when it combines with them. It lowers the value of Arc and Speck. The combination value in two cases is intermediate between that of the single mutations. In the other two cases it is lower than either component. See Figs. 4 and 5.

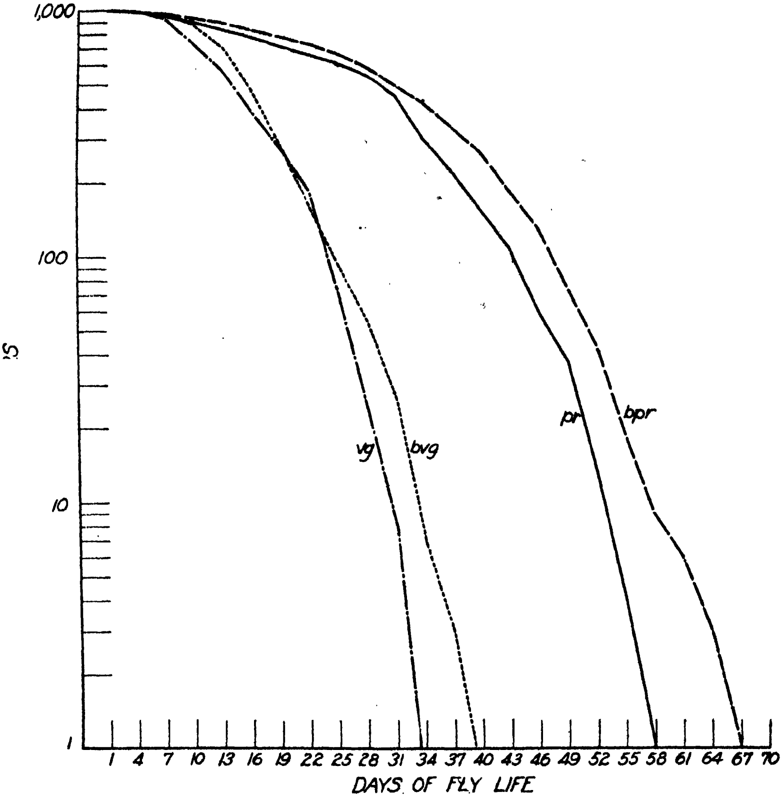

FIG. 4. Male $l_x$ lines comparing *bpr* with *pr*, and *b vg* with *vg*.

Combining Purple with the others we have:

TABLE XII

| Strain | Mean Duration of Life | Strain | Mean Duration of Life | Difference |
|---|---|---|---|---|
| Purple | 27.42±.27 | | | |
| Black | 41.02±.53 | Purple-black | 30.44±.34 | —10.58±.63 |
| Vestigial | 14.98±.28 | Purple-vestigial | 11.72±.13 | — 3.26±.31 |
| Arc | 25.20±.33 | Purple-arc | 36.00±.53 | +10.80±.62 |
| Speck | 46.63±.63 | Purple-speck | 23.72±.22 | —22.91±.67 |

In this case Purple raised the value of Arc and lowered that of Black, Vestigial and Speck. In only a single instance in the above is the combination value intermediate.

Combining Vestigial with the others we have:

TABLE XIII

| Strain | Mean Duration of Life | Strain | Mean Duration of Life | Difference |
|---|---|---|---|---|
| Vestigial | 14.98±.28 | | | |
| Black | 41.02±.53 | Vestigial-black | 16.45±.23 | —24.57±.58 |
| Purple | 27.42±.27 | Vestigial-purple | 11.72±.13 | —15.70±.30 |
| Arc-speck | 38.41±.58 | Vestigial-arc-speck | 12.81±.26 | —25.00±.64 |

Vestigial-black is the only combination intermediate between that of the single mutants above. Both Vestigial-purple and Vestigial-arc-speck have lower values than their components. It was not practicable to make combinations with Arc and Speck separately, due to the masking effect of Vestigial on Arc. In every case above

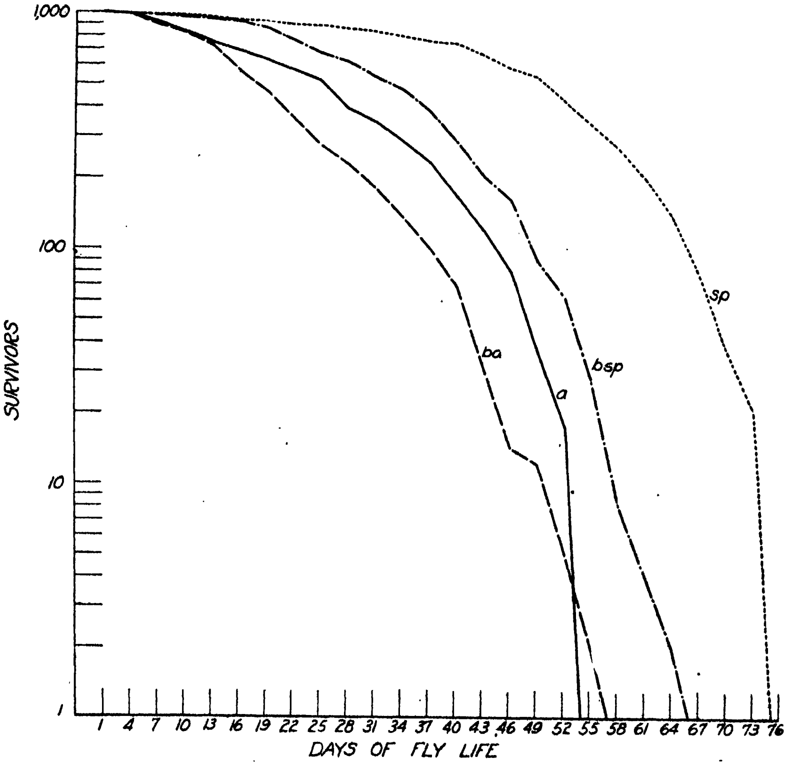

FIG. 5. Male $l_x$ lines comparing *b sp* with *sp*, and *b a* with *a*.

Vestigial reduced the value of the other character in the combination.

From the foregoing it is evident that the duration of life of combinations is not always, nor even generally, the average of the single mutants entering in it. Also, there is interaction between different mutants which seems to be definite, if correctly understood or interpreted.

The differences noted above are all significant from the standpoint of probability. The least significant difference noted is four times its probable error (see Vestigial vs. Black-vestigial). However, since we are dealing with extremely variable material (see table of biometric constants) and in all sorts of combinations, it is best not to attach undue importance to small differences in order that we may appreciate the meaning of the larger differences.

Some facts are outstanding from the data presented above which we now propose to examine further.

1. Whenever Vestigial is at all present in a strain the value of the combination is about the same as or lower than that of Vestigial alone. This further reduction seems to be dependent on the other mutants present, Purple and Speck. Black raises the value of Vestigial to a slight extent.

TABLE XIV

| Strains | Mean Duration of Life | Difference |
|---|---|---|
| Vestigial | *14.98*±*.28* | |
| Black-vestigial | 16.45±.23 | +1.47±.36 |
| Purple-vestigial | 11.72±.13 | —3.26±.31 |
| Black-purple-vestigial-arc/ | 14.79±.16 | — .19±.32 |
| Vestigial-arc-speck | 12.81±.26 | —2.17±.38 |
| Black-vestigial-arc-speck | 13.97±.26 | —1.01±.38 |
| Purple-vestigial-speck | 9.47±.17 | —5.51±.33 |
| Black-purple-vestigial-arc-speck | 9.45±.17 | —5.53±.33 |

Vestigial then may be recognized as the most powerful single factor in determining duration of life among the mutants studied. It overshadows the effect of the other characters, although its prepotency, if such we may call it, is not complete. See Figs. 6 and 7.

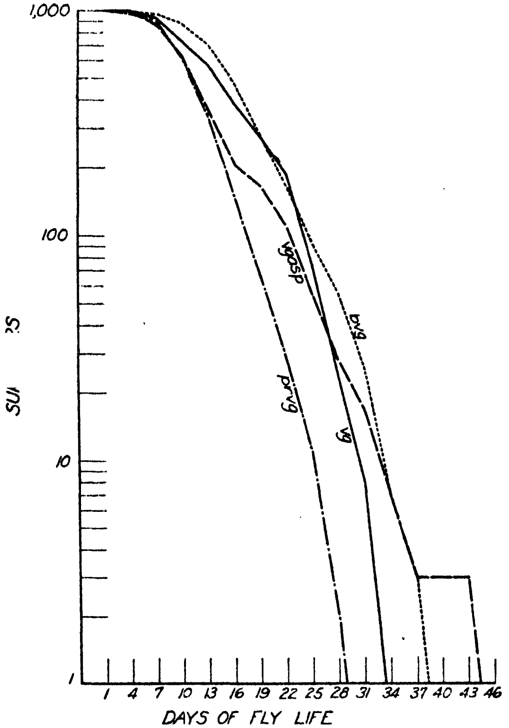

FIG. 6. Male $l_x$ lines of stocks containing vestigial. Two mutations.

2. Whenever Vestigial is absent, Purple is the prepotent gene; that is, when present in combination with the other mutant genes, it tends either to raise or lower the value of the combination to its level. See Fig. 8.

TABLE XV

| Strains | Mean Duration of Life | Difference |
|---|---|---|
| Purple | 27.42±.27 | |
| Black-purple | 30.44±.34 | + 3.02±.43 |
| Purple-arc | 36.00±.53 | + 8.58±.60 |
| Purple-speck | 23.72±.22 | — 3.70±.35 |
| Black-purple-arc | 35.06±.55 | + 7.64±.61 |
| Black-purple-speck | 31.22±.45 | + 3.80±.52 |
| Purple-arc-speck | 38.38±.62 | +10.96±.68 |
| Black-purple-arc-speck | 22.65±.42 | — 4.77±.50 |

Purple is sensibly raised by Black and Arc, especially the latter, and lowered by Speck. The effect of Arc on Purple is a little unusual, since Arc by itself has a lower mean duration of life than Purple.

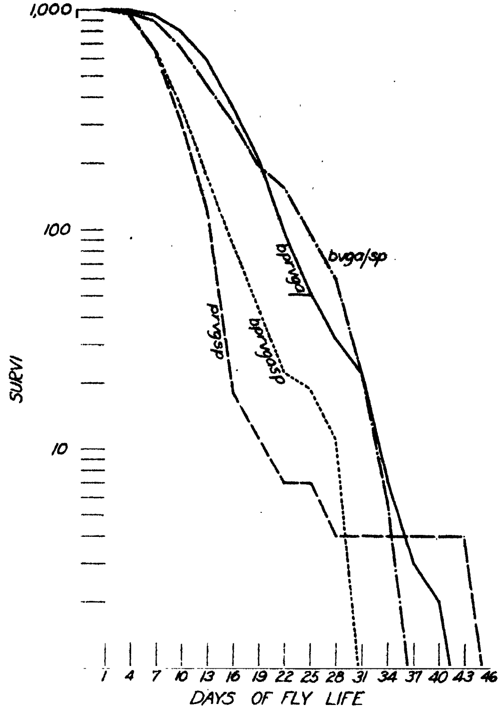

FIG. 7. Male $l_x$ lines of stocks containing vestigial. Three or more mutants.

3. Arc is a strong modifier of the values of the other mutants. It increases the value of Purple and lowers that of Black and Speck, when taken alone.

TABLE XVI

| Strains | | Original Strain + Arc | | Difference |
|---|---|---|---|---|
| pr | 27.42±.27 | pr a | 36.00±.53 | + 8.58±.60 |
| bpr | 30.44±.34 | bpr a | 35.06±.55 | + 4.62±.65 |
| pr sp | 23.72±.22 | pr asp | 38.38±.62 | +14.66±.66 |
| vg | 14.98±.28 | vgasp | 12.81±.26 | — 2.17±.38 |
| bpr sp | 31.22±.45 | bpr asp | 22.65±.42 | — 8.57±.61 |
| b | 41.03±.53 | b a | 20.11±.36 | —20.92±.64 |
| sp | 46.63±.63 | asp | 38.41±.58 | — 8.22±.86 |
| b sp | 32.36±.35 | b asp | 33.72±.53 | + 1.36±.64 |

4. Black and Speck, when alone, give flies with long duration of life, longer in fact than the Wild males. In combination the resulting strain has a lower duration of life than either component mutant. See Fig. 9. Their reaction with other mutants has already been noted in the individual discussion of such mutants.

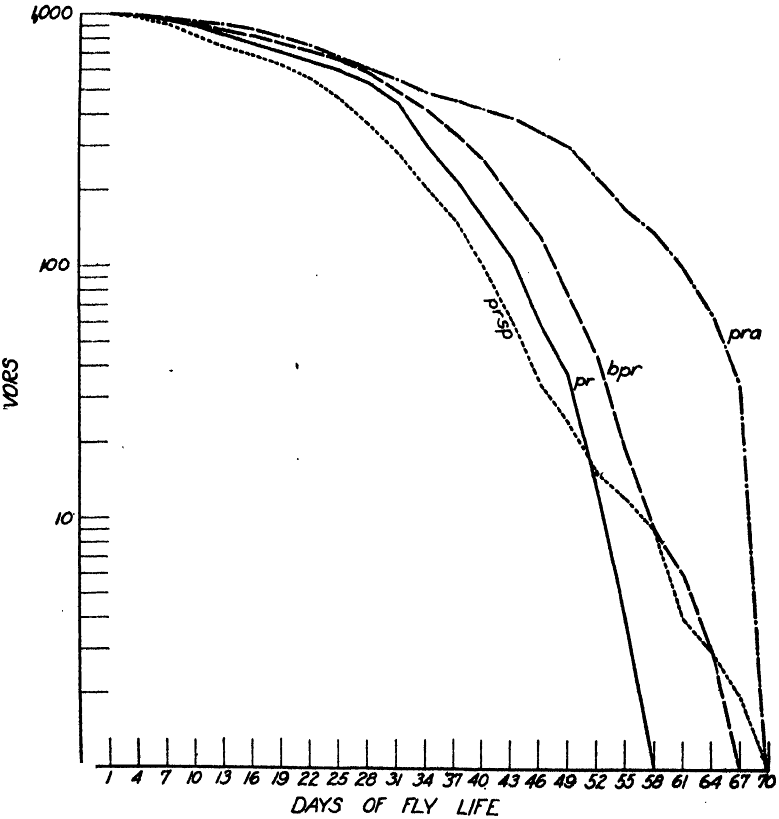

FIG. 8. Male $l_x$ lines of stocks containing purple combinations, without vestigial.

## INHERITANCE OF DURATION OF LIFE IN FEMALES

Duration of life in the females should not differ materially from that of males after due correction is made for the differences in influence of sex, if the behavior of the genes is definite in respect of duration of life. In other words, should we plot the survivorship lines of males and females of the same strain, they should run virtually parallel to each other, maintaining a distance equal to the difference due to sex, but otherwise describing the same type of curve.

We shall test this for the five single mutants.

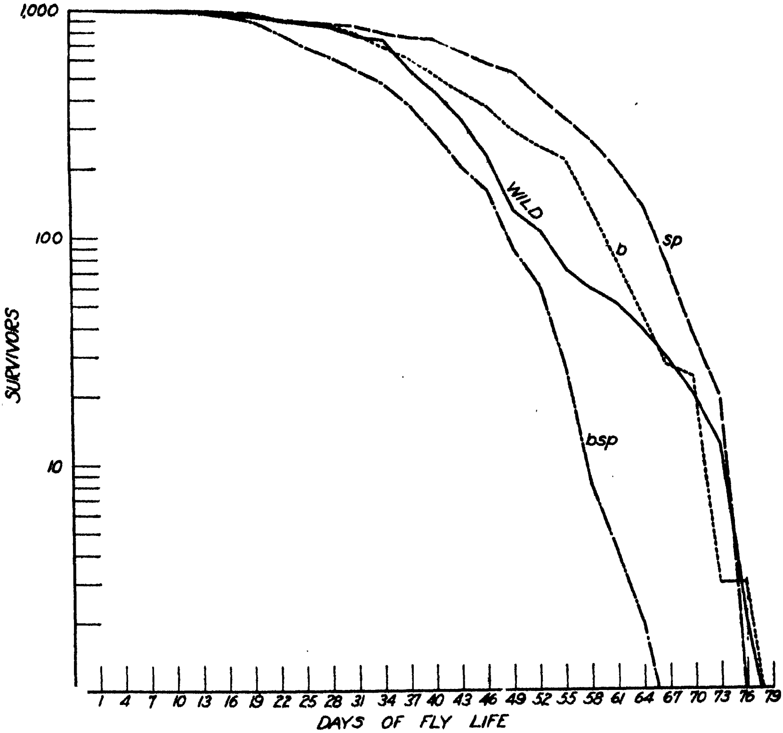

FIG. 9. Male $l_x$ lines of *b* and *sp* compared with wild and their combination *b sp*.

Our data in Table VI show us that in:

| | |
|---|---|
| Black—there is a non-significant difference between males and females of | 0.70 ± .74 days |
| Purple—males are longer lived by | 5.59 ± .35 days |
| Vestigial—females are longer lived by | 6.00 ± .49 days |
| Arc—females are longer lived by | 3.04 ± .50 days |
| Speck—males are longer lived by | 7.72 ± .91 days |

Figs. 10 and 11 show that our assumption as to the effect of sex is essentially correct for Black, Purple, Vestigial and Speck. The case of Arc is a little different.

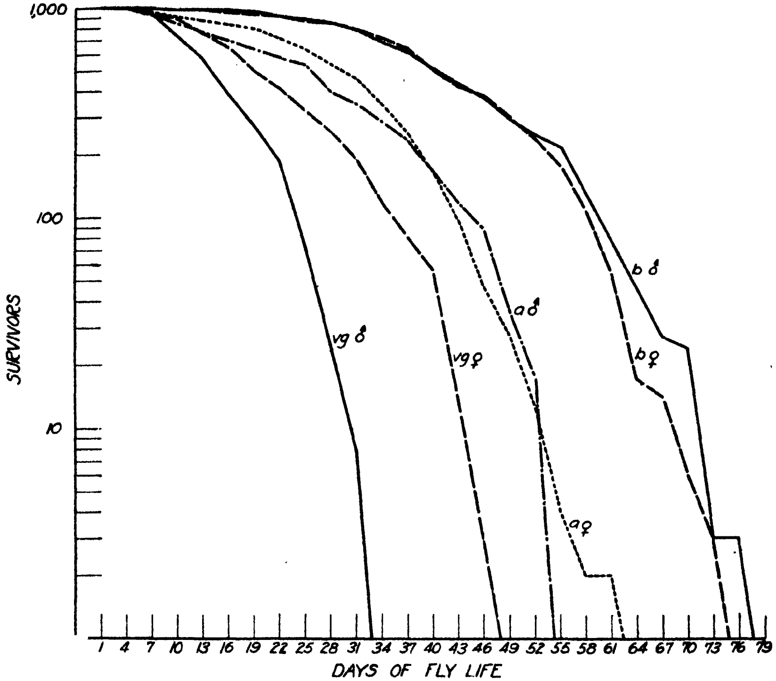

FIG. 10. Survivorship lines of *b*, *a*, and *vg*, males and females compared.

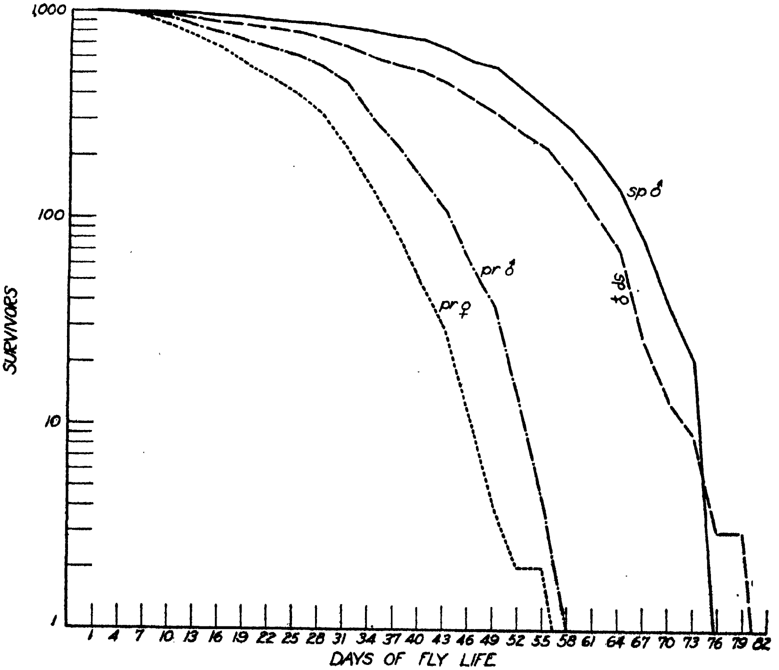

**FIG. 11.** **Survivorship lines of *pr* and *sp*, males and females compared.**

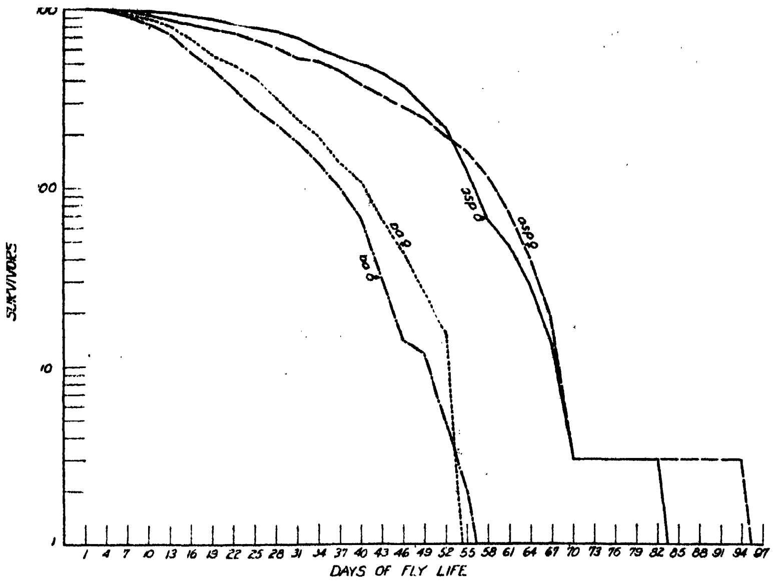

FIG. 12. Survivorship lines of Arc combinations, *b a* and *asp*, comparing male and female lines.

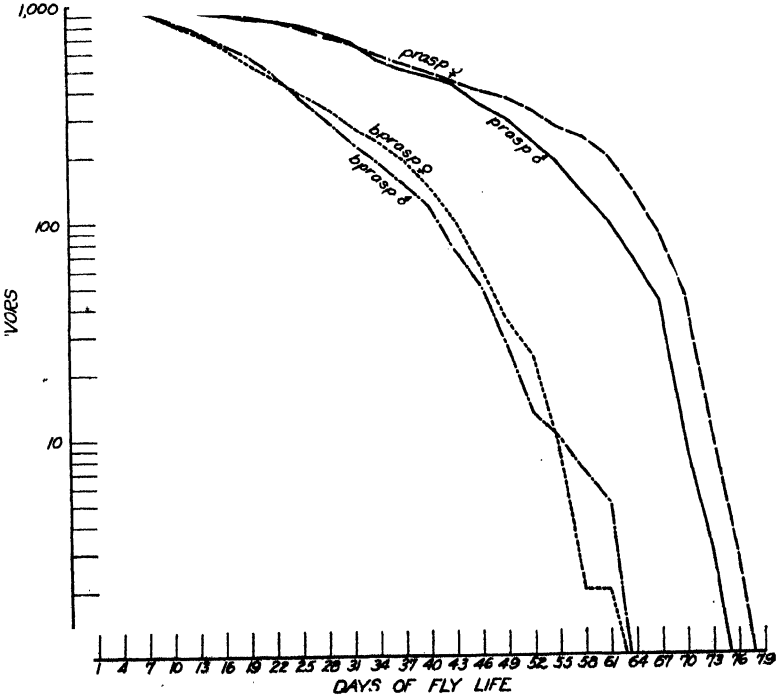

FIG. 13. Survivorship lines of Arc combinations, *pr asp* and *bpr asp*, comparing male and female lines.

In this there is a heavy mortality of males in early and later life and a low one in middle life. The case is reversed in the females, with the result that the curves cross and re-cross each other. This behavior of Arc is felt more or less in some of its combinations, as may be seen from Figs. 12 and 13, but not sufficiently to modify the general results. This characteristic of Arc, together with its property of being recessive in general yet a powerful modifier, suggests the possibility of its being a gene different in nature from the other mutations studied.

The survivorship data of the different female strains are given in Tables 17, 18 and 19, the distributions being on the basis of 1000, as in all previous tables.

TABLE XVII

SURVIVORSHIP DISTRIBUTION OF FEMALES OF ORIGINAL STOCKS AND STRAINS INVOLVING SINGLE MUTATIONS

| Age in Days | Number of Survivors up to Indicated Age | | | | | | |
|---|---|---|---|---|---|---|---|
| | Wild | Quintuple | Black | Purple | Vestigial | Arc | Speck |
| 1 | 1000 | 1000 | 1000 | 1000 | 1000 | 1000 | 1000 |
| 4 | 997 | 957 | 989 | 996 | 993 | 983 | 981 |
| 7 | 987 | 707 | 983 | 921 | 951 | 953 | 969 |
| 10 | 960 | 483 | 972 | 844 | 878 | 904 | 947 |
| 13 | 932 | 352 | 963 | 749 | 750 | 868 | 906 |
| 16 | 871 | 240 | 938 | 655 | 649 | 823 | 868 |
| 19 | 857 | 176 | 913 | 543 | 497 | 781 | 846 |
| 22 | 842 | 121 | 885 | 468 | 410 | 704 | 814 |
| 25 | 812 | 74 | 845 | 395 | 319 | 628 | 780 |
| 28 | 780 | 48 | 825 | 319 | 257 | 528 | 733 |
| 31 | 731 | 24 | 772 | 235 | 187 | 455 | 670 |
| 34 | 695 | 12 | 701 | 139 | 115 | 345 | 594 |
| 37 | 635 | 10 | 631 | 84 | 80 | 251 | 541 |
| 40 | 593 | 2 | 501 | 48 | 56 | 164 | 506 |
| 43 | 504 | 0 | 414 | 29 | 14 | 98 | 443 |
| 46 | 441 | — | 375 | 11 | 3 | 47 | 371 |
| 49 | 345 | — | 296 | 4 | 0 | 28 | 314 |
| 52 | 268 | — | 234 | 2 | — | 13 | 255 |
| 55 | 154 | — | 175 | 2 | — | 4 | 217 |
| 58 | 112 | — | 107 | 0 | — | 2 | 154 |
| 61 | 81 | — | 54 | — | — | 2 | 104 |
| 64 | 50 | — | 17 | — | — | 0 | 69 |
| 67 | 34 | — | 14 | — | — | — | 25 |
| 70 | 21 | — | 6 | — | — | — | 13 |
| 73 | 4 | — | 3 | — | — | — | 9 |
| 76 | 0 | — | 0 | — | — | — | 3 |
| 79 | — | — | — | — | — | — | 3 |
| 82 | — | — | — | — | — | — | 0 |
| Abs. No of flies | 676 | 420 | 355 | 1006 | 288 | 470 | 318 |

## TABLE XVIII

### SURVIVORSHIP DISTRIBUTION OF FEMALES OF STRAINS INVOLVING TWO MUTATIONS

| Age in Days | Number of Survivors up to Indicated Age | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | bpr | b vg | b a | b sp | prvg | pr a | pr sp | asp |
| 1 | 1000 | 1000 | 1000 | 1000 | 1000 | 1000 | 1000 | 1000 |
| 4 | 990 | 982 | 981 | 992 | 981 | 1000 | 967 | 994 |
| 7 | 943 | 969 | 938 | 978 | 931 | 969 | 919 | 972 |
| 10 | 807 | 912 | 878 | 962 | 836 | 929 | 839 | 919 |
| 13 | 722 | 820 | 800 | 942 | 706 | 893 | 757 | 869 |
| 16 | 638 | 735 | 680 | 899 | 566 | 819 | 673 | 816 |
| 19 | 577 | 647 | 556 | 842 | 436 | 752 | 608 | 769 |
| 22 | 526 | 536 | 489 | 759 | 335 | 683 | 527 | 732 |
| 25 | 459 | 451 | 416 | 634 | 245 | 603 | 433 | 670 |
| 28 | 390 | 363 | 318 | 531 | 203 | 535 | 338 | 611 |
| 31 | 319 | 291 | 242 | 453 | 149 | 465 | 265 | 539 |
| 34 | 255 | 209 | 193 | 371 | 82 | 400 | 192 | 508 |
| 37 | 196 | 147 | 137 | 275 | 33 | 342 | 141 | 452 |
| 40 | 141 | 90 | 109 | 178 | 11 | 304 | 83 | 377 |
| 43 | 97 | 46 | 67 | 116 | 4 | 258 | 43 | 330 |
| 46 | 62 | 15 | 43 | 90 | 2 | 227 | 22 | 283 |
| 49 | 32 | 8 | 26 | 67 | 0 | 189 | 8 | 249 |
| 52 | 24 | 8 | 15 | 53 | — | 140 | 5 | 196 |
| 55 | 5 | 5 | 0 | 13 | — | 104 | 2 | 162 |
| 58 | 4 | 0 | — | 3 | — | 83 | 0 | 118 |
| 61 | 1 | — | — | 0 | — | 57 | — | 75 |
| 64 | 1 | — | — | — | — | 49 | — | 40 |
| 67 | 0 | — | — | — | — | 28 | — | 19 |
| 70 | — | — | — | — | — | 0 | — | 3 |
| 73 | — | — | — | — | — | — | — | 3 |
| 76 | — | — | — | — | — | — | — | 3 |
| 79 | — | — | — | — | — | — | — | 3 |
| 82 | — | — | — | — | — | — | — | 3 |
| 85 | — | — | — | — | — | — | — | 3 |
| 88 | — | — | — | — | — | — | — | 3 |
| 91 | — | — | — | — | — | — | — | 3 |
| 94 | — | — | — | — | — | — | — | 3 |
| 97 | — | — | — | — | — | — | — | 0 |
| Abs. No. of flies | 787 | 388 | 466 | 601 | 523 | 652 | 1750 | 321 |

## TABLE XIX

SURVIVORSHIP DISTRIBUTION OF FEMALES OF STRAINS INVOLVING THREE AND FOUR MUTATIONS

| Age in Days | Number of Survivors up to Indicated Age | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | bpr a | bpr sp | b asp | pr asp | vgasp | prvg sp | bprvg / a | b vga / sp | bpr asp |
| 1 | 1000 | 1000 | 1000 | 1000 | 1000 | 1000 | 1000 | 1000 | 1000 |
| 4 | 995 | 966 | 985 | 997 | 986 | 974 | 989 | 974 | 977 |
| 7 | 976 | 910 | 963 | 992 | 939 | 801 | 953 | 886 | 922 |
| 10 | 920 | 833 | 885 | 963 | 842 | 540 | 880 | 804 | 819 |
| 13 | 862 | 732 | 826 | 928 | 710 | 354 | 776 | 693 | 733 |
| 16 | 808 | 655 | 741 | 902 | 620 | 189 | 687 | 562 | 637 |
| 19 | 753 | 595 | 674 | 875 | 559 | 126 | 565 | 454 | 533 |
| 22 | 700 | 532 | 615 | 832 | 509 | 83 | 458 | 363 | 451 |
| 25 | 638 | 486 | 537 | 774 | 455 | 56 | 367 | 288 | 384 |
| 28 | 552 | 401 | 456 | 702 | 409 | 36 | 287 | 206 | 333 |
| 31 | 449 | 346 | 378 | 649 | 380 | 33 | 211 | 160 | 274 |
| 34 | 378 | 264 | 326 | 582 | 312 | 17 | 157 | 108 | 234 |
| 37 | 308 | 215 | 267 | 527 | 247 | 10 | 114 | 82 | 193 |
| 40 | 256 | 152 | 189 | 487 | 183 | 3 | 67 | 52 | 146 |
| 43 | 199 | 95 | 126 | 434 | 133 | 0 | 26 | 26 | 102 |
| 46 | 164 | 54 | 78 | 396 | 104 | — | 5 | 16 | 61 |
| 49 | 124 | 40 | 41 | 367 | 97 | — | 3 | 10 | 35 |
| 52 | 94 | 22 | 15 | 322 | 54 | — | 3 | 3 | 24 |
| 55 | 61 | 11 | 0 | 269 | 29 | — | 2 | 0 | 9 |
| 58 | 49 | 3 | — | 242 | 25 | — | 2 | — | 2 |
| 61 | 35 | 2 | — | 199 | 11 | — | 2 | — | 2 |
| 64 | 28 | 2 | — | 138 | 4 | — | 2 | — | 0 |
| 67 | 23 | 0 | — | 88 | 0 | — | 2 | — | — |
| 70 | 12 | — | — | 45 | — | — | 2 | — | — |
| 73 | 3 | — | — | 11 | — | — | 2 | — | — |
| 76 | 0 | — | — | 3 | — | — | 2 | — | — |
| 79 | — | — | — | 0 | — | — | 0 | — | — |
| Abs. No. of flies | 574 | 624 | 270 | 376 | 279 | 302 | 616 | 306 | 576 |

The frequency constants are given in Table XX.

TABLE XX

BIOMETRIC CONSTANTS FOR DURATION OF LIFE OF DIFFERENT STRAINS OF FEMALE DROSOPHILA

| Strains | Number of flies | Mean (in days) | Standard Deviation (in days) | Coefficient of Variation |
|---|---|---|---|---|
| Wild | 676 | 40.62±.42 | 16.14±.30 | 39.74± .84 |
| bprvgasp (Quintuple) | 420 | 12.12±.25 | 7.50±.17 | 61.90±1.91 |
| b | 355 | 40.33±.51 | 14.20±.36 | 35.20±1.00 |
| pr | 1006 | 21.83±.23 | 10.76±.16 | 49.30± .90 |
| vg | 288 | 20.98±.40 | 9.95±.28 | 47.45±1.61 |
| a | 470 | 28.24±.37 | 11.89±.26 | 42.09±1.08 |
| sp | 318 | 38.91±.65 | 17.32±.46 | 44.52±1.41 |
| bpr | 787 | 24.06±.32 | 13.33±.23 | 55.39±1.20 |
| b vg | 388 | 24.20±.40 | 10.78±.26 | 44.56±1.28 |
| b a | 466 | 23.17±.37 | 11.80±.26 | 50.93±1.39 |
| b sp | 601 | 29.97±.31 | 11.44±.22 | 38.18± .84 |
| prvg | 523 | 19.05±.27 | 9.27±.19 | 48.65±1.23 |
| pr a | 652 | 31.98±.43 | 16.36±.31 | 51.15±1.18 |
| pr sp | 1750 | 22.96±.19 | 11.68±.13 | 50.89± .71 |
| asp | 321 | 34.69±.66 | 17.55±.47 | 50.58±1.66 |
| bpr a | 574 | 30.56±.42 | 14.99±.30 | 49.05±1.19 |
| bpr sp | 624 | 24.45±.37 | 13.59±.26 | 55.59±1.35 |
| b asp | 270 | 26.80±.53 | 12.95±.38 | 48.32±1.70 |
| pr asp | 376 | 40.67±.45 | 18.44±.64 | 45.34±1.33 |
| vgasp | 279 | 25.20±.61 | 15.11±.43 | 59.95±2.24 |
| prvg sp | 302 | 12.17±.26 | 6.77±.19 | 55.61±1.94 |
| bprvga/ | 616 | 22.18±.29 | 10.64±.20 | 47.95±1.11 |
| b vga/sp | 306 | 19.56±.41 | 10.75±.29 | 54.95±1.90 |
| bpr asp | 576 | 23.11±.38 | 13.37±.27 | 57.85±1.49 |

Using the same method of examination as in males, we have:

TABLE XXI

| Strains | Mean Duration of Life | Difference |
|---|---|---|
| Vestigial | *20.98±.40* | |
| Black-vestigial | 24.20±.40 | +3.22±.57 |
| Purple-vestigial | 19.05±.27 | —1.93±.48 |
| Black-purple-vestigial-arc/ | 22.18±.29 | +1.20±.49 |
| Vestigial-arc-speck | 25.20±.61 | +4.22±.73 |
| Black-vestigial-arc-speck | 19.56±.41 | —1.42±.57 |
| Purple-vestigial-speck | 12.17±.26 | —8.81±.48 |
| Black-purple-vestigial-arc-speck | 12.12±.25 | —8.86±.47 |

The above table shows that the results with Vestigial in the female are on the whole the same as those in the male; that is, Vestigial operates to reduce the longevity values of the mutants with which it has entered into combination to its general level. There is considerable variation, though, as its effects are modified to some extent by the other mutants, as in the case of the males. Purple and Speck tend to reduce the duration of life of the combinations further, while Black tends to raise it.

Table XXII shows the effect of Purple on the other mutants whenever Vestigial is absent.

TABLE XXII

| Strains | Mean Duration of Life | Difference |
|---|---|---|
| Purple | *21.83±.23* | |
| Black-purple | 24.06±.32 | + 2.23±.39 |
| Purple-arc | 31.98±.43 | +10.15±.49 |
| Purple-speck | 22.96±.19 | + 1.13±.30 |
| Black-purple-arc | 30.56±.42 | + 8.73±.48 |
| Black-purple-speck | 24.45±.37 | + 2.62±.44 |
| Purple-arc-speck | 40.67±.45 | +18.84±.51 |
| Black-purple-arc-speck | 23.11±.38 | + 1.28±.45 |

As in the males, the effect of Purple is not as pronounced as that of Vestigial, being modified considerably by the other mutations. The direction of these modifications is in the majority of cases consistent with that found in the males. Black, and especially Arc, raises its value, while Speck without a third character has little effect. See Figs. 14 and 15.

Arc also acts as a non-prepotent gene in general, in the sense that it does not bring the value of its combinations to its level, but, as in the male, it increases the value of Purple and Vestigial and lowers that of Black and Speck. The following table is illuminating on this point:

TABLE XXIII

| Strain | | Strain + arc | | Difference |
|---|---|---|---|---|
| pr | 21.83±.23 | pr a | 31.98±.43 | +10.15±.49 |
| bpr | 24.06±.32 | bpr a | 30.56±.42 | + 6.50±.53 |
| pr sp | 22.96±.19 | pr asp | 40.67±.45 | +17.71±.49 |
| vg | 20.98±.40 | vgasp | 25.20±.61 | + 4.22±.73 |
| bpr sp | 24.45±.37 | bpr asp | 23.11±.38 | — 1.34±.53 |
| b | 40.33±.51 | b a | 23.17±.37 | —17.16±.63 |
| sp | 38.91±.65 | asp | 34.69±.66 | — 4.22±.93 |
| b sp | 29.97±.31 | b asp | 26.80±.53 | — 3.17± 61 |

Black and Speck, individually, have as high a duration of life as the Wild stock. The two in combination give a lower duration of life than either of them alone. They together may be considered as relatively impotent, in the sense that their combinations follow the general level of duration of life of the other genes present rather than of their own. When not together, however, they have a tendency to raise the duration of life of certain combinations in which they take part above that of the other mutant when alone.

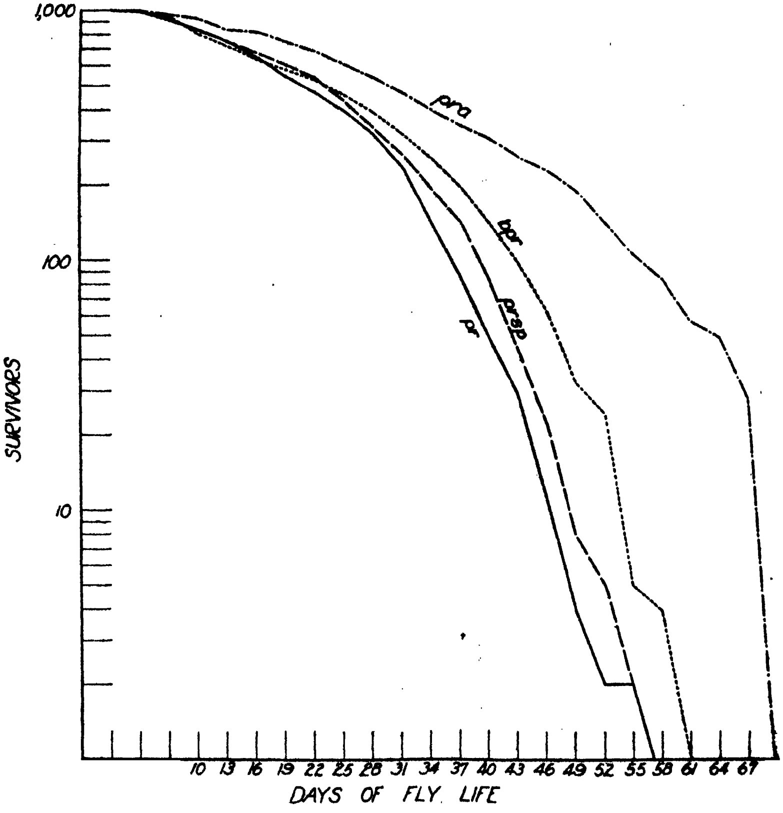

FIG. 14. Female $l_x$ lines of purple combinations. Two mutations.

## Discussion of Results

As a first attempt in relating duration of life to particular genes these experiments have perhaps had their greatest usefulness in outlining future lines of endeavor, by having demonstrated that certain phenomena likely to be supposed to be concerned with duration of life have no influence over it at all. A number of theories have come to the mind of the writer during the course of these experiments, suggested mostly by the general behavior of factors already well understood. A brief mention of these will be made, as by a process of elimination of what duration of life *is not* influenced by, we may be led closer and closer to the narrower path of what *is* important in determining it.

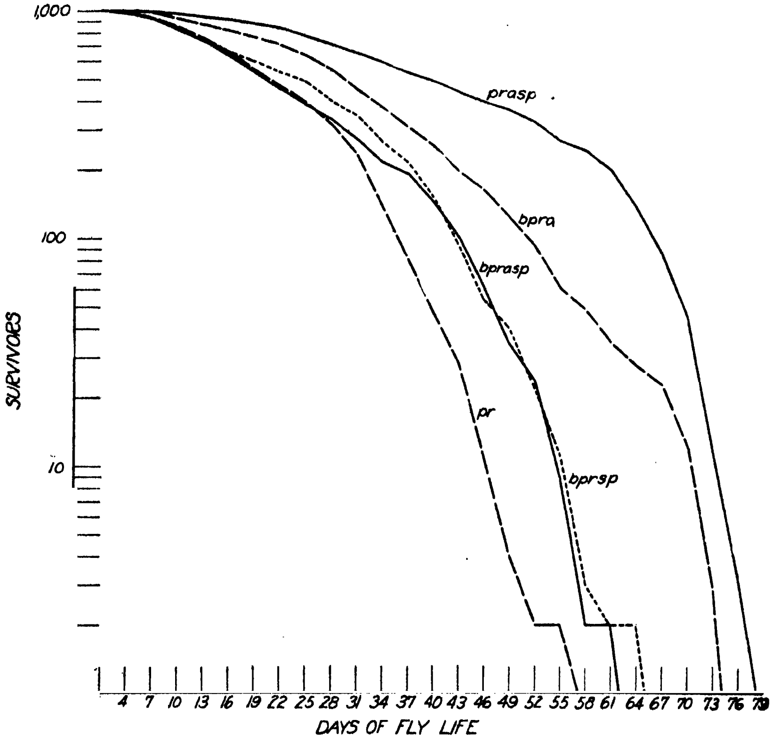

FIG. 15. Female $l_x$ lines of purple combinations. Three or more mutations.

1. *Influence of Number of "Irregular Links."* Mutations by their nature and the circumstances of their appearance may be considered as due to "abnormal" genes. If we accept Morgan's theory of linear arrange-

ment of genes, and picture the chromosomes as consisting of a string of "beads," each representing a gene, it is easy to conceive of an "abnormal bead" causing a weak link on both sides of it. If each irregular link should affect duration of life adversely, we should expect a corresponding shortening of the duration of life with the addition of each mutant gene. In other words, the number of irregular links being directly dependent on the number of these new genes, the duration of life of the resulting strain should be inversely proportional to the number of mutations it has. Our results have shown that there is no foundation for this belief, as the *number of mutant genes in a strain has no relation per se to its duration of life.*

2. *Influence of Number of Mutations.* Similarly, it is of common observation that mutants in general are not as viable, nor as fertile, nor as long lived as the wild stocks of *Drosophila.* The wild stock has been regarded as the standard, and the addition of any mutation generally lowers this standard. Sometimes it does not affect it, but I have not hitherto seen a case recorded of a mutation affecting fertility and duration of life favorably. An increase in the number of mutations in a chain might be expected to be followed by a corresponding reduction in the vital properties of the individuals. Our data show that duration of life does not primarily depend on the number of mutations in a strain, but rather on the intrinsic properties of the mutations present in it.

3. *Blending Effects of Mutant Genes.* If a number of mutant genes are known to affect duration of life definitely and yet are independent of each other, one may conceive of their behaving in this fashion: (a) The resulting combination of two or more mutants would give a duration of life which is the average of the components; or (b) if each mutant may be regarded as increasing or decreasing duration of life so many days from the standard, a combination strain would give the algebraic sum of the value of each mutation with the normal duration

of life. Neither of these alternatives is supported by the results. A good illustration is found in the case of Black and Speck. Individually they have either no effect, or increase duration of life over that of the wild strain; in combination they shorten duration of life.

4. *Physiological Effect of Mutant Genes.* Among the mutants studied Vestigial has the greatest effect on duration of life, and it so happens that it is the external character that affects most the general behavior of the fly by curtailing its normal activity. One may easily conclude that it is this physical defect, if we may regard it as so, that is the direct cause of the shortening of the duration of life of those strains containing the character Vestigial. This view has been demonstrated by Pearl *et al.* (57) to be erroneous. The duration of life of wild flies the wings of which were clipped was compared with normal ones. The results show a slightly longer duration of life in the normal ones, but not sufficient to account for the big difference between Wild and Vestigial. This small difference may properly be attributed to the injury caused to the flies in handling and clipping their young wings and in causing an open wound in the vein severed.

If further proof is necessary on this point, we have the case of Purple. This is a mutation affecting eye color, which in so far as it is possible to observe has no other effect in the physical make-up of the flies, and yet it affects duration of life to a very marked extent.

There is, therefore, a more fundamental reason for the differences in the duration of life of these mutants than any of those suggested above.

What, then, is the possible explanation?

In examining our data critically we are forced to conclude that the different mutants whose duration of life has been the object of this study behave as units in so far as this character is concerned. This behavior is as distinct and regular as the external appearance of the character which serves as an "earmark" for the identification of the gene which determines the somatic manifestation of each.

The question is whether the factors for duration of life are located in the very gene of each of the mutants studied, or whether they are separate genes, completely or very closely linked to these mutant genes. It is not probable that the five mutations picked at random as subjects for this study should, each and every one of them, be linked to a separate determiner for duration of life. We have had several years' experience in the laboratory with Vestigial stock, which contains the factor affecting duration of life most, either pure or in crosses, and involving several thousand individuals, and we have yet to find a Vestigial fly living beyond the regular span established by this character. If the gene for duration of life were a distinct and separate entity we should expect to have seen a certain proportion of long-lived Vestigial flies due to cross-overs, however small that proportion might be. The assumption, therefore, that the duration of life factors reside in the very genes of the mutants studied seems to be the more plausible and logical.

Morgan and his students have found about fifty factors that affect eye color alone. In this one study of an apparently more complicated character, in five mutants taken at random, all were found to affect duration of life. It is not too much to presume that there are many more which equally affect duration of life.

We have called attention to the fact that there is an appreciable prepotency of certain genes over others in respect of their effect upon duration of life. Such effects may be construed as of the same nature as the effects produced by the presence of a number of factors controlling the same organ but located in different parts of a chromosome or even in different chromosomes. Numerous examples are found in the mutant eye colors and wing lengths of *Drosophila*. Sometimes there is complete prepotency, as in the case of Vestigial hiding the presence of Arc absolutely; sometimes there is blending, as in the effect of Vermilion, a factor for eye color in the fifth chromosome, on Purple, another eye color factor in the second chromosome. There are all kinds of gradations in the interaction of such factors. In our material presented above there is variety enough to overtax the descriptive words of Morgan such as "modifiers," "disproportionate modifiers," "differentiators," "sensitizers," etc.

It is a well-known fact among geneticists, especially those working with *Drosophila,* that the designation of any mutant race, White eye, for example, has reference only to that characteristic of it which is readily discernible. It is also regarded as a fact that the productivity and viability of such an individual is affected adversely as compared with the wild fly. Morgan goes a little further and states that "The productivity of the individual (of any mutant)[4] is also much affected and the viability is lower than in the wild fly." While we do not subscribe entirely to that statement, inasmuch as our data show that there is at least one mutant which actually increases duration of life, it is apparently true in more cases than it is not true. Morgan continues: "It follows that whatever it is in the germ plasm that produces white eyes also produces other modifications as well, and modifies not only such 'superficial' things as color, but also such 'fundamental' things as productivity and viability." Such being the case, the name applied to the factor is only useful in designating the conglomerate of effects which behave as a single unit in inheritance, and we may perfectly well call the separate duration of life factors recognized in these experiments "Duration of Life factor 1, 2, 3, 4 and 5," each respectively associated with visible modifications Black, Purple, Vestigial, Arc and Speck. Logically, such naming of these mutants is as sound and justifiable as to name them on the basis of morphological differences.

## SUMMARY AND CONCLUSIONS

This paper is a first attempt at localizing in the chromosomes factors controlling duration of life. Five mutants in the second chromosome of *Drosophila melanogaster* were used as indices for five distinct factors that were recognized as having definite effects on duration of life. The five mutants were contained originally in one parent strain, which, crossed with the wild stock, produced twenty-two distinct combinations. The behavior of these combinations with respect to duration of life was studied in a total of 24,287 flies.

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[4] The parenthetic expression is added to clarify the reference.

It is shown that under constant environmental conditions, definite degrees of duration of life are associated with extreme precision and exactness with the presence or absence of certain genes in the chromosomes. These same genes also control certain morphological characters. Through the biometric treatment of the data a better insight is obtained of the interactions of factors present in different parts of the chromosome affecting the same property of the individual than has been possible with such characters as eye color and length of wing not susceptible to fine measurement.

It is also shown that some of the factors, although not sex linked, affect the sexes differently.

The above statements rest on the assumption that the units in the wild fly that are allelomorphs to the mutant genes influence or control the same characters.

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(The plan of numbering citations is explained in the second of these Studies, AMER. NAT., Vol. 56, p. 174.)

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# FAMILY RESEMBLANCES AMONG AMERICAN MEN OF SCIENCE

DR. DEAN R. BRIMHALL
SECRETARY OF THE PSYCHOLOGICAL CORPORATION

## IV. RESEMBLANCE AND THE DEGREE OF DISTINCTION

IT will be remembered that the starred men were arranged in an order of merit by statistical methods. In this arrangement the total number falls into four convenient groups:

> These are: I. those among the leading hundred of our scientific men; II. those among the second and third hundreds; III. those below this rank in the thousand; IV. those who in the second arrangement fell below the thousand, * * *. The first three groups cover about equal ranges of merit, and this also holds in a general way for the fourth group.[1]

The positions attained are not permanent. Men advance or lose in relative position according to the merit of their performance as judged by their fellows. Whatever the variability of the position may be it seems desirable to determine the family resemblance of the different groups owing to the unique fact of the order of merit arrangement, an order that has definite objective validity.

Table XV gives the results of the comparison of the four groups according to the number with relatives of distinction.

TABLE XV

| Groups | I | II | III | IV | Total |
|---|---|---|---|---|---|
| Number in each group who replied.......... | 78 | 174 | 552 | 152 | 956 |
| Number with relatives of distinction...... | 25 | 57 | 137 | 37 | 256 |
| Per cent. with distinguished relatives... | 32.1 | 32.8 | 24.8 | 24.3 | 26.8 |

The two upper groups have in proportion to their numbers more among them with relatives of distinction. Aside from the first group the per cent. is progressively less for the four groups. Since the positions are variable and the numbers in the different groups small it is interesting that these dissimilarities should be found. If groups one and two are combined and compared with three and four combined, the validity of the comparison should be increased; the numbers in the two groups are larger and the possibility of variability of position lessened. This arrangement makes a comparison of approximately the upper quarter with the lower three quarters. Thirty-two and five tenths per cent. of the 252 in the upper quarter and 24.7 per cent. of the lower three quarters had relatives of distinction. Seventy-six per cent. as many of the men from the lower three quarters as from the upper quarter are thus represented by relatives as defined. The validity of this ratio of 4 to 3 is not known but may be inferred from the probable errors of similar ratios in the table XVII.

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[1] Cattell, *Pop. Sci. Monthly*, May, 1915.

Table XVI gives the comparison of the four groups in terms of the number of relatives of distinction instead of scientific men found to have such.

TABLE XVI

| Groups | I | II | III | IV | Total |
|---|---|---|---|---|---|
| Number of replies | 78 | 174 | 552 | 152 | 956 |
| Number of relatives of distinction | 45 | 105 | 278 | 70 | 498 |
| Number of distinguished relatives per hundred replies | 57.7 | 60.3 | 50.4 | 46.0 | 52.1 |

The differences have the same ranking order as those shown in table XV; the value for group one is slightly less than group two and groups three and four are progressively smaller than two or one. Compared as two groups those from the upper quarter have 59.5 and the lower three quarters 49.4 relatives per hundred men reporting. The larger group has 83 per cent. as many as the smaller or "upper quarter" group.

Table XVII gives the distribution of relatives according to the relationship and distinction of the men whose relatives they are. In this table the upper quarter is compared with the lower three quarters.

TABLE XVII

| Relationship. | Number of relatives per 100 men reporting. Upper quarter. | Lower three quarters. | Per cent. values of column two in terms of column one. |
|---|---|---|---|
| Brothers and sisters | 20.24 | 15.34 | 76 |
| Sons, daughters, nieces and nephews | 3.97 | 2.98 | 75 |
| Parents | 10.32 | 7.81 | 76 |
| Uncles and aunts | 7.54 | 6.96 | 92 |
| Grandparents | 6.35 | 5.40 | 85 |
| Cousins | 11.11 | 10.94 | 99 |
| Total | 59.53 | 49.43 | 83 ± 2.56 |

The results show an almost perfect 4–3 ratio for the three groups of near relatives and it is just those relationships that are the most significant. There is no valid difference shown in the cousin relationship. If these differences are due primarily to environmental factors, or to organic, or in part to both, it is important that we know it, but first of all it is important that we know such differences exist.

## SUMMARY

The results show (1) that 32.5 per cent. of those in the upper quarter and 24.7 per cent. of those in the lower three quarters of the starred group have relatives of distinction as defined; (2) that the lower three quarters have 83 ± 2.56 per cent. as many relatives of distinction as the upper quarter.

## V. THE SPECIALIZATION OF RESEMBLANCE

Table XVIII gives the distribution of relatives of men of science according to kinship and number who are distinguished for work in science. Those found only in "American Men of Science" have been omitted from this table owing to the constant error in favor of the workers in science that such inclusion would make.

TABLE XVIII

| Relationship. | Total number of Distinguished Relatives. | Number of Workers in Science. | Per cent. |
|---|---|---|---|
| Brothers and sisters | 140 | 60 | 43 |
| Sons and daughters | 14 | 12 | 86 |
| Nieces and nephews | 11 | 6 | 55 |
| Parents | 78 | 30 | 38 |
| Uncles and aunts | 68 | 16 | 24 |
| Grandparents | 54 | 13 | 24 |
| Cousins | 100 | 42 | 42 |
| Total | 465 | 179 | 38± 5.3 |

About 43 per cent. of the 140 comparable brothers and sisters are known for their work in science. Almost the same ratio holds for cousins. That for the parents seems to be less but it is really greater since the handbook from which most of the latter biographies come has about half the relative number of people of science that "Who's Who in America" has. The same is somewhat true for the aunts, uncles and grandparents. The number of workers in science included in Appleton's Cyclopedia was estimated by counting the number in the first five hundred. This number proved to be 37, or 7.4 per cent. of the total.

The striking resemblance in the case of the sons and daughters is probably not of valid significance owing to the small number of cases. That such resemblance should exist now when science is super-respectable is to be expected, but that it should exist in the grandparent relationship is certainly interesting, especially since 10 of the 13 grandfathers are fathers of the mothers of the men of science. Eight of the 13 are known for work in the same or closely allied sciences in which their grandsons have won renown.

Any thorough-going investigation of specialization of resemblance would require a clear definition of the function to be measured and a scale for use in measuring the amount found in any individual. There should be, say, a knowledge of what one means by astronomy and an accomplishment test by which any astronomer's work could be measured. Obviously no such exact methods are available. We can, therefore, do no better than use these terms in the usual commonsense meaning and assume they represent somewhat similar performance. This is confessedly a rough and imperfect method and will probably become increasingly so owing to the increased overlapping of the different sciences.

No little effort was made to arrive at some method of grouping the sciences according to a classification that takes care of the overlapping. That finally adopted divides the twelve general divisions into two groups, (1) those of the more mathematical or physical sciences, (2)

TABLE XIX

DISTRIBUTION OF DISTINGUISHED RELATIVES OF MEN OF SCIENCE ACCORDING TO THE DIRECTION OF THEIR WORK AND THE DIRECTION OF THE WORK OF THE MEN WHOSE RELATIVES THEY ARE

| | Direction of Work of the Men of Science Who Have Distinguished Relatives | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Direction of work of distinguished relatives | Astron. | Chem. | Geol. | Math. | Physics | Anat. | Anth. | Bot. | Path. | Physiol. | Psychol. | Zool. | Total |
| Astr. | 4.5 | 1.0 | | .5 | 1.0 | | | | .3 | | .5 | | 7.8 |
| Chem. | | 10.0 | 4.5 | .5 | 3.5 | | .5 | 1.0 | 2.0 | | | 4.5 | 26.5 |
| Geol. | | 4.5 | 14.5 | 1.0 | 2.5 | | | | 1.0 | 2.0 | .3 | 2.0 | 27.8 |
| Math. | | 1.0 | 1.0 | 3.0 | 1.5 | | | .3 | | | .5 | .5 | 7.8 |
| Physics | 1.0 | 4.5 | .8 | 1.5 | 18.3 | | 1.5 | 2.3 | 3.3 | .5 | 2.0 | 5.5 | 41.2 |
| Anat. | 1.0 | 4.0 | 1.3 | | .8 | 4.0 | | 1.0 | 6.5 | 1.0 | .5 | 2.3 | 22.4 |
| Anth. | 1.0 | 1.3 | 1.2 | | | | | | 1.3 | 1.0 | .5 | 1.8 | 8.1 |
| Botany | 1.0 | 5.5 | | | 4.0 | 1.0 | | 12.0 | 1.5 | | 1.5 | 1.0 | 27.5 |
| Path. | | 2.8 | 2.3 | .5 | 6.8 | | | 1.0 | 5.3 | 3.0 | 1.5 | 3.8 | 27.0 |
| Psychol. | | | | | | | | | 1.3 | | 3.0 | 1.0 | 5.3 |
| Zool. | | 2.5 | 1.0 | | 3.5 | 1.0 | | 3.0 | 1.3 | .5 | | 9.0 | 21.8 |
| Art | 1.0 | 5.0 | 3.0 | 1.0 | 2.0 | | | | 1.5 | 2.0 | | 4.0 | 19.5 |
| Educ. | 1.8 | 5.2 | 2.3 | 1.5 | 1.7 | 2.0 | 1.0 | 1.3 | 1.0 | 1.0 | 4.5 | 3.0 | 26.3 |
| Physiol. | | | | | 1.0 | | 1.0 | | | .5 | | .5 | 3.0 |
| Invent. | | .5 | | | .3 | | | | | | | | .8 |
| Law | | 13.0 | 4.8 | 1.0 | 10.5 | | | 2.5 | 6.3 | | 3.0 | 6.8 | 47.9 |
| Lit. | 1.8 | 10.2 | 11.0 | 6.0 | 9.5 | | 1.0 | 5.8 | 3.1 | 2.0 | 3.5 | 10.5 | 64.4 |
| Polit. | 2.4 | 4.5 | 2.3 | 8.5 | 5.3 | .5 | | .5 | .3 | .5 | 2.0 | .8 | 27.6 |
| Relig. | 1.0 | 10.7 | 11.4 | 1.0 | 5.8 | | | 1.3 | .8 | 4.0 | 3.0 | 5.7 | 44.7 |
| Trade | .5 | 5.3 | 2.8 | 1.0 | 3.5 | .5 | | 3.0 | 1.5 | 1.5 | 1.7 | 2.0 | 23.3 |
| War | | 4.5 | .8 | 1.0 | .5 | 2.0 | | 1.0 | .7 | .5 | | 6.3 | 17.3 |
| Totals | 17.0 | 96.0 | 65.0 | 28.0 | 82.0 | 11.0 | 5.0 | 36.0 | 39.0 | 20.0 | 28.0 | 71.0 | 498.0 |

those of the biological sciences. Astronomy, chemistry, geology, mathematics and physics make up the first group and anatomy, anthropology, botany, pathology, physiology, psychology and zoology the second. It may be that the geologists are somewhat misplaced; if so, they would, it seems, be more misplaced if put with the biological sciences.

Table XIX gives the distribution of relatives according to the direction of their work and according to the work of the scientific men whose relatives they are. If a relative is known for work in two directions each is given a fractional value of one half; if in three directions each is given a value of one third.

The first column gives the distribution of 17 relatives of astronomers. Four and five tenths is the value for the number distinguished in astronomy, 1 in physics, 1 in anatomy, 1 in anthropology, 1 in botany, 1 in art and so on. The second column gives a similar distribution of 96 relatives of the chemists. The others follow in order.

The details of table XIX are given more objective form in table XX. Here, instead of the raw numbers and details within each group the per cent. values of the three groups are given in a form that makes direct comparison possible. The astronomers, for example, have

### TABLE XX

#### PHYSICAL SCIENCES

| | Astron. | Chem. | Geol. | Math. | Physics | Total |
|---|---|---|---|---|---|---|
| Physical sciences | 32 | 22 | 32 | 23 | 33 | 28 ± 1.5 |
| Biological sciences | 18 | 17 | 9 | 2 | 20 | 14 ± 2.0 |
| Fields other than science | 50 | 61 | 59 | 75 | 47 | 58 ± 3.0 |
| Total | 100 | 100 | 100 | 100 | 100 | 100 |

#### BIOLOGICAL SCIENCES

| | Anat. and Anthrop. | Bot. | Path. | Psychol. | Physiol. | Zool. | Total |
|---|---|---|---|---|---|---|---|
| Physical sciences | 12 | 10 | 17 | 13 | 12 | 18 | 15 ± .7 |
| Biological sciences | 44 | 47 | 44 | 30 | 25 | 27 | 35 ± 2.4 |
| Fields other than science | 44 | 43 | 39 | 57 | 63 | 55 | 50 ± 2.4 |
| Total | 100 | 100 | 100 | 100 | 100 | 100 | 100 |

17 relatives, of whom 32 per cent. belong to the physical science group, 18 per cent. to the biological sciences and 50 per cent. to the group "other fields than science."

Fifty-six per cent. of the 956 men in the group belong to the physical sciences and 44 to the biological sciences. This is the distribution for the thousand and is the approximate distribution for the workers recorded in "American Men of Science." There were, therefore, at the time of the study more workers in the physical sciences than in the biological in about a 5 to 4 ratio. Instead of the ratio that might be expected as a matter of chance, namely, the 5 to 4, there is a 2 to 1 relationship with significant reliability for the relatives of the physical science group and a 3 to 7 relationship for the biological sciences. It seems incredible that these resemblances in the direction of work of a group of scientific men and their near relatives should be due to organic resemblance. However, the resemblances are there whatever the valid explanation.

Lester F. Ward, the great apostle of the doctrine of the effectiveness of environment in controlling human conduct, says:

> In certain of the arts special aptitudes are of course presupposed, and this is probably true for that great art called literature, but in the various sciences, outside of mathematics, this is not so much the case and almost any one with proper training and adequate facilities can prosecute scientific researches.[2]

A somewhat similar opinion concerning mathematics has been expressed by Cattell, as follows:

> My general opinion is that certain aptitudes, as for mathematics and music, are mainly innate, and that kinds of character and degree of ability are mainly innate, but that the direction of the performance is mainly due to the circumstances and that environment imposes a veto on any performance not congenial to it.[3]

It may be "that almost any one with proper training and adequate facilities can prosecute scientific researches," but the results of this study show that the relatives of scientific men are many times as likely to do so as men of the generality. Brothers, for example, of men of special performance in science are over 200 times as likely to show special performance in science. Moreover, near relatives are more than twice as likely to follow a dissimilar field as defined.

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[2] Ward, Dynamic Psychology, p. 241.

[3] *Science*, N. S., Vol. 24, pp. 732–744.

What of the dissimilarities? It may be that the congenital equipment which determines the performance in fields other than mathematics is also somewhat unitary, thus allowing unusual success in literature, law, education, politics, trade, science and the like. Why, for example, should the mathematicians be well represented in the field of politics, particularly diplomacy? Of their 28 distinguished relatives more are distinguished in this direction than in all the sciences; in literature they have a value of 6 and in mathematics only 3. If Galton had examined the relatives of his judges, he would no doubt have found some well known for their work in literature or politics or other fields into which their opportunities had led them. Even the men of science who are included in this study as members of the starred group are by no means limited in their special achievement to the science in question. Dean Roscoe Pound, of Harvard, is internationally known for his work as a lawyer. He is an educational administrator of recognized merit. His sister is distinguished in literature. What is one to say about the specialization of resemblance here?

I doubt if there is a family here reported in which the performance of the various individuals is not different in kind. The astronomers, for example, have three families, the Pickerings, the Searles and the Doolittles, whose work is primarily in astronomy. But, one member of the first is known for his work in ethnology and botany and one of the second is known for his work in religion. The distinguished relatives of Percival Lowell run almost the entire gamut; the brother of Ormond Stone was the head of the great Associated Press news-gathering system. Certainly these differences are as striking as the similarities that have been expressed as averages, or as the individual cases as they stand in the lists of names. The botanists, on the other hand, have a great array of resemblances in the specific field of botany.

In discussing the number of workers in religion whose offspring became men of science, Galton says:

> Can then religion and science be in harmony? It is true that their methods are different; the religious man is attached by his heart to his religion, and can not bear to hear its truth discussed, and he fears scientific discoveries which might in some slight way discredit what he holds more important than all the rest. The scientific man seeks truth regardless of consequences * * *. These are indeed important differences, but the two characters have one powerful element in common. Neither the religious nor the scientific man will consent to sacrifice his opinions to material gain, to political ends, nor to pleasure. *Both agree in the love of intellectual pursuits* and in the practice of a simple, regular, laborious life, and both work in a disinterested way for the public good.[4]

The italics in the above quotation are the present writer's. There may be, and probably are, different kinds of intelligences. Just as there are *memories,* rather than *memory,* there are various types of intellectual performance, but these types, whatever they are, must have many elements in common. The lawyer, the minister, the educator and the man of science must respond to fine differences and shades of differences. Similarities in the finer elements of situations must be seen. The average child of three can not respond to the element or concept of "fourness." He may be able to respond by the concept "more-than-two." If he is found to respond not only to "fourness" in a group of objects of that number but to "fiveness" or "sixness" we are justified in considering him gifted in ability to do intellectual operations involving number concepts.

Professor Woodworth, in his book "Dynamic Psychology," shows how Newton recognized a similarity between the falling apple and the moon revolving about the earth. There are many persons who can not respond to this similarity with the aid of skilled teachers. So, "if the environment places a veto on any activity not congenial to it'' the intellectual capacity places a veto on any environment not congenial to it. If the writer understands Professor Woodworth's argument, the mere possession of a capacity tends to its expression because the organism is ''set'' toward a certain activity and continues in a state of dissatisfaction until the reaction for which it is organized and prepared by original nature is in operation. Thus, if a person is so organized that he forms language habits easily and quickly he will take pleasure in forming them, if he is able to see differences in plant and animal growth, human behavior, and the like, he is ill at ease unless he is so doing and is satisfied when so doing.

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[4] Galton, "On the causes which operate to create scientific men," *Fortnightly Review,* Vol. XIX, pp. 345–351.

If it be assumed that the performance of the individual is predicated on his congenital equipment there is still the question of how far that equipment will resemble the equipment of other individuals coming from the same or nearly related groups of germ cells. The resemblances of persons in closely related groups have been measured and shown to be many times greater than the resemblance of people chosen at random. What these resemblances mean may be left for future investigations. If society can increase its workers in science over 200 times by giving all children the same average advantages that the brothers of men of science are thought to have had, one answer is obvious. Whatever the explanation, there is no mistaking the implication that the people from the professional classes, and most of all men of science, should be given every opportunity to raise large families. The fact remains that the near relatives of these men produce far more than their share of the best that civilization offers, and it should be made easy for them to reproduce themselves, at least, until more of society can enjoy the supposed privileges enjoyed by the professional classes.

## SUMMARY

The resutls show (1) that 38 ± 5.3 per cent. of the distingiushed relatives of men of science show special performance in science, which is about three times that of the distinguished people of the generality as recorded by "Who's Who in America," (2) that there is specialized resemblance in the direction of the kind of science, physical and biological—instead of the distribution of 5 relatives in the physical sciences to 4 in the biological which is the distribution in "American Men of Science," the men from the physical sciences have 2 relatives in the physical sciences to 1 in the biological, while the men of science in the biological group have 3 relatives in the physical to 7 in the biological, (3) that the dissimilarities offer perplexing data if one is to assume that resemblances are due to unitary factors of organic equipment.

## VI. THE RELATIVES OF WIVES OF MEN OF SCIENCE: ASSORTIVE MATING

The two quotations given below, one from Galton and one from Ward, throw into relief an interesting question of fact. Galton claims to have been impressed with the evidence in biographical accounts of eminent men of assortive mating in the direction of intellect. He says:

> The great fact remains that able men take pleasure in the society of intelligent women, and, if they can find such as would in other respects be suitable, they will marry them in preference to mediocrities.[5]

Ward, the great proponent of the doctrine that genius is "in things" rather than men, says:

> The children of an eminent man are only half his. Half of every one of them belongs to his wife. And who is his wife? A person from entirely different stock. As geniuses are rare at best, the chances are enormously against her being a genius too. But there is a law of nature that partners choose their opposites. Galton is not ignorant of this law but he questions it.[6]

Here we have objective evidence, and to an extent in quantitative form, that Galton was correct. And who are the wives of the men of science? Of 919 of them, 57 are daughters of distinguished fathers, some of whom are world celebrities. Twenty-one of the wives are themselves women of distinction; 48 are sisters of men of distinction; 55 are nieces of distinguished men and 26 are granddaughters of the same sort, nor do these exhaust the relationships as table XXII shows.

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[5] Hereditary Genius, 1892, p. 316.

[6] Lester F. Ward, Applied Sociology, p. 119.

Denial of assortive mating is not the only mistake of the sociologists. Ignoring it has resulted in misinterpreting apparent evidence of persistence of desirable traits coming from one individual. Consider the following in this connection:

> Remember the size, ages and financial conditions of the family when the father died—the sons being aged eight, eighteen and thirty—and then consider the fact that the three sons graduated from Princeton, and five of the daughters married college graduates, three of them Yale, and one of them Harvard and one of Princeton.[7]

The point made is that in spite of unusual obstacles three sons of the famous Jonathan Edwards graduated from college and five of the daughters showed special performance by marrying college men. It is not unlikely that the performance of the husbands of the five daughters was equal to that of the three brothers and that hereditary characters of equal value were carried by husbands and wives. Even a casual reading of the history of the Edwards family will show how a considerable portion of the stock might have been kept up by such marriages as the five original daughters made. And what of the Jukes?

### The Number of Distinguished Wives

Of the 956 men concerned, 84 were reported as unmarried, 43 are known to have been married twice and two were married three times. At the time the data were gathered there had been, therefore, 919 marriages. Of these, 21 were with women of distinction as defined. Among the records of the men who did not report, 3 other wives of distinction were noted owing to cross relationship with members of the starred group. Fourteen of the 21 wives are recorded in "Who's Who in America" and 14 in "American Men of Science"; 3 of the latter being in the starred group. Fourteen are distinguished for work in science and 6 in literature.

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[7] Winship, Jukes-Edwards, 1900, p. 33.

It is not known how many of the women who are recorded in the various handbooks are married but a good many certainly are not. The number of women in "Who's Who in America" is about ten per cent. of that of the men. If every 1,000 men of the generality, belonging to the same age group as the men of science, had among them 14 distinguished wives the handbook containing their biographies would have to have nearly 200,000 accounts of married women of distinction. It is doubtful whether any volume of "Who's Who" used in this study had more than 1,000 such accounts.

### DISTINGUISHED RELATIVES OF WIVES

Table XXI gives the details of the distribution of the wives and their relatives (1) according to the direction of the work of their husbands, (2) according to the number having relatives of distinction, (3) according to the number of distinguished relatives.

TABLE XXI

| Direction of husband's work | (1) Total wives | Wives with distinguished relatives | Distinguished relatives |
|---|---|---|---|
| Astronomy | 42 | 8 | 15 |
| Chemistry | 158 | 22 | 42 |
| Geology | 85 | 19 | 32 |
| Mathematics | 75 | 8 | 20 |
| Physics | 151 | 25 | 42 |
| Anatomy | 25 | 1 | 2 |
| Anthropology | 16 | 1 | 2 |
| Botany | 93 | 13 | 18 |
| Pathology | 53 | 14 | 31 |
| Physiology | 36 | 7 | 11 |
| Psychology | 39 | 4 | 10 |
| Zoology | 146 | 25 | 48 |
| Total | 919 | 147 | 273 |

The figures of table XXI show that 147, or about one in six, of the 919 women had relatives of distinction equal to that of their husbands. Sixteen of the 147 are represented only by children and as there may be some doubt as to the validity of the comparisons which include the children when the fathers are of known distinction this number may be subtracted, making the ratio about one in seven for the number with distinguished relatives. This is more than one half as great as that of the men themselves. One hundred and thirty-one women have 254 or 1.93 relatives per individual; this is equivalent to the 1.95 ± .06 per individual for their husbands.

TABLE XXII

| | | Handbooks | | | |
|---|---|---|---|---|---|
| Relationship | Total | Am. Men of Science | Who's Who | Appleton's | Starred group |
| B | 48 | 18 | 47 | 4 | 11 |
| Si | 10 | | 10 | | |
| S | 18 | 15 | 13 | | 5 |
| D | 1 | | 1 | | |
| F | 57 | 12 | 35 | 40 | 10 |
| M | 3 | | | 3 | |
| FB | 28 | 1 | 4 | 27 | |
| FSi | 2 | | 1 | 2 | |
| MB | 27 | 6 | 15 | 13 | 2 |
| MSi | | | | | |
| BS | 3 | 1 | 3 | | 1 |
| BD | | | | | |
| SiS | 1 | | 1 | | |
| SiD | 1 | | 1 | | |
| FF | 15 | | 1 | 15 | |
| FM | | | | | |
| MF | 11 | | 1 | 10 | |
| MM | | | | | |
| FBS | 17 | 2 | 11 | 10 | 1 |
| FBD | 2 | | 2 | | |
| FSiS | 5 | 2 | 4 | | |
| FSiD | | | | | |
| MBS | 14 | 3 | 10 | 4 | 3 |
| MBD | 1 | | 1 | | |
| MSiS | 9 | 5 | 7 | 2 | 4 |
| MSiD | | | | | |
| Total | 273 | 65 | 168 | 130 | 37 |

Table XXII gives the distribution of the relatives of the 147 wives (1) according to kinship, (2) according to the handbook or handbooks in which they are found reported, (3) according to the number in the starred group. Table XXIII gives a comparison of the per cents. in each handbook and in the starred group in comparison with similar data on the husbands' relatives.

TABLE XXIII

| Relatives of men of science | Am. Men of Science | Who's Who in Am. | Appleton's Cyclopedia | Starred group |
|---|---|---|---|---|
| 498 | 28 | 62 | 40 | 11 |
| Relatives of wives | | | | |
| 273 | 24 | 62 | 48 | 14 |

Contrary to expectation "American Men of Science" and the starred group do not have a significantly greater representation among the relatives of the men of science, that is, greater in proportion to the total number of distinguished relatives.

### Distinguished Brothers

It is not known how comparable the brothers of the wives are with the brothers of the men of science. Assuming the two groups to be directly comparable the figures show that the brother of a wife of a man of science is about one third as likely to be known for unusual performance as a brother of a man of science. That is, 956 men of science are known to have 146 distinguished brothers; 919 of the wives have 48 such brothers. For the men of science the ratio is about 6.5 to 1; for the wives, 19.2 to 1. Since the brother of a man of science is found to be 73 times as likely as a man of the generality to be included in the handbook, "Who's Who in America," a brother of his wife would be about 24 times as likely to be included. This proportion probably errs in a negative direction. The brothers of the wives are as a group younger than the brothers of the men of science and it is likely that the data on the former group are much less complete than on the latter. Ten of the wives' sisters are distinguished and 13 of the sisters of the men of science.

### Other Relatives

The relative number of distinguished parents is greater than the number of brothers. The men have 78 fathers and 3 mothers of note; the women have 57 fathers and 3 such mothers. The wives have approximately 2 fathers of distinction for 3 such fathers which the husbands have. The uncles and aunts, grandparents and cousins are represented by the numbers 68, 54, 105 for the men, and 57, 26, 48 for the wives. It is obvious that the large differences are in the remote relationships and may be accepted as evidence of greater incompleteness in the data on the relatives of the wives.

### SPECIALIZATION IN DIRECTION OF WORK

Not only are men of science likely to choose wives who on the average have more than half as many distinguished relatives as they have themselves but they are likely to choose wives whose relatives show special performance in science. Table XXIV shows the facts for the distribution of the relatives of the wives according to the degree of kinship and according to the number known for work in science. Eighty-eight, or 33 per cent., not counting those found only in "American Men of Science," of the 273 have done work in science. This compares with 38 per cent. for the same data concerning the men of science, a difference much smaller than one might expect.

TABLE XXIV

NUMBER AND PER CENT. DISTINGUISHED IN SCIENCE

| Relationship | Total | Number in science | Per cent. in science |
|---|---|---|---|
| Brothers and sisters | 58 | 24 | 41 |
| Sons and daughters | 14 | 12 | 86 |
| Parents | 60 | 25 | 42 |
| Uncles and aunts | 56 | 12 | 21 |
| Nephews and nieces | 5 | 1 | 20 |
| Grandparents | 26 | 4 | 15 |
| Cousins | 46 | 10 | 22 |
| Total | 265 | 88 | 33 ± 5.9 |

The relative number of brothers in the two groups is exactly in the ratio of 1 to 1, that is, 24 in science and 24 in fields other than science; for fathers it is 1 to 1.3; for uncles, 1 to 3.8; grandparents, 1 to 6.5, and for first cousins, male, it is 1 to 4.3. These interesting results show resemblances that increase with nearness of relationship although the different groups are not strictly comparable.

Aside from the supposition that men of intellect are attracted by women similarly gifted it is reasonable to suppose that this apparent specialization of resemblance is the result of propinquity. During the mating period sisters of colleagues or daughters of professors are likely to be companions in laboratories and social activities.

### DISTINCTION AND DEGREE OF KINSHIP

Table XXV gives the distribution of the male relatives of the wives, (1) according to a coarse grouping of the number in each degree of kinship, (2) the number in each degree of kinship expressed in comparable ratio with the number in the brother relationship, (3) the same ratios expressed in the per cent. that each is of the sum of all of them.[8]

TABLE XXV

| | Total | Comparable ratios | Ratios in per cents. |
|---|---|---|---|
| Brothers | 48 | 48 | 33.4 |
| Fathers | 57 | 57 | 39.7 |
| Uncles | 55 | 27.5 | 19.1 |
| Cousins | 45 | 11.25 | 7.8 |
| Total | 205 | 143.75 | 100 |

With the exception of the brother-father relationships the results are in agreement with those found for the men of science themselves. As has been said, the brother relationship may be incomplete in that those in this degree were too young to have had time to show their performance, or owing to the mechanics of the handbooks and incompleteness of the data reported by the men or to both.

### THE WIVES OF THE ZOOLOGISTS

There is a curious distribution of distinguished wives of men of science. The zoologists have 10 of the 21 who are included in the statistical data. The marital condition of 144 of the zoologists at the time of the investigation was as follows: 7 were unmarried, 7 had been married twice, 1 had been married three times, making 146 marriages in all. Among these 146, 10 were with women who were or later became distinguished as defined. Eight are listed as workers in zoology, 1 in psychology and 1 in literature.

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[8] See section III for explanation of method of determination of ratios.

This may be a chance result. The fact that the number of distinguished relatives of the wives of the zoologists is proportionately about the same as that found for each of the other sciences would seem to make it so. In any event the data are interesting in connection with the following:

> Francis Galton long ago pointed out the good results of a custom obtaining in Germany, whereby college professors tended to marry the daughters or sisters of college professors. A tendency of men of science to marry women of scientific attainments or training is marked among biologists, at least, in the United States * * *.[9]

Here we have, probably for the first time, objective evidence that zoologists tend to marry women of scientific attainments or training and that men of science, in general, tend to marry women who come from families of special intellectual performance, particularly in the direction of science.

Perhaps in the near future society will know exactly the chances of obtaining superior individuals from particular matings, assuming that it knows what superior individuals are like. It is not inconceivable that even a democracy will learn to pay a bonus for children from certain matings, trusting to the possibility of persistence of desirable traits in the same. Such a practice would facilitate the rearing and bearing of children of men and women of science if our data mean what they seem to. Now that there is evidence that men and women of science intermarry, thus increasing the chances of offspring resembling them, the suggestion of a bonus should seem less bizarre than upon first thought.

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[9] Popenoe and Johnson, Applied Eugenics, 1918, p. 228.

## SUMMARY

The data in this chapter have shown (1) that a distinguished man of science is at least 200 times as likely to have a distinguished wife as a man of the generality, (2) that the direction of the performance of the wife is likely to be in science or literature, (3) excluding children, that approximately 1 in 7 of the wives has one or more relatives of distinction, which is more than half as many as the men themselves have, (4) that specialization in resemblance is shown by the fact that 33 per cent. of the distinguished relatives of the wives and 38 per cent. of the same for the men are known for their work in science, (5) that the number of distinguished relatives varies with the degree of remoteness of relationship except in the father-brother groups, (6) that the zoologists have a disproportionate share of the distinguished wives.

# A LETHAL GENE IN FOWLS[1]

DR. L. C. DUNN
STORRS AGRICULTURAL EXPERIMENT STATION

SOME evidence has been secured bearing on the occurrence and inheritance of a lethal gene in fowls which appears to be closely or completely linked with a gene (c) which determines the difference between colored and recessive white plumage. Although the hypothesis offered has not been sufficiently tested, it is desired to record the present data, since the stock carrying the assumed lethal is nearly extinct and may yield no further information.

The first indications of the presence of such a gene appeared in the results obtained by crossing a Pit Game male of unknown breeding with White Wyandotte females. The $F_1$ generation from this cross consisted entirely of colored fowls (77). Several male offspring were crossed each with his own mother and with his full sisters, producing an $F_2$ generation consisting of 105 colored and 33 white (expected 103.5: 34.5) and a backcross generation consisting of 51 colored and 29 white (equality expected). The deficiency of whites in this generation was found to be due principally to abnormal ratios in the progeny of two $F_1$ males. One of these males bred to his mother produced 19 colored and 8 white chicks (equality expected). By five $F_1$ sisters he gave a normal ratio (17 colored: 5 white). In the next season this male was bred to all his surviving relatives. Mortality in this stock was extremely high and his only surviving relatives were a daughter (colored Cc), a half sister (colored Cc) and the following white fowls: a niece, 2 aunts and 3 cousins, the latter having come from the same purebred Wyandotte stock to which his mother belonged.

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[1] Contributions in Genetics No. 18, Storrs Agricultural Experiment Station.

The results of these matings were as follows:

TABLE I

RESULTS OF MATING $F_1$ MALE 104 (Cc) WITH VARIOUS RELATIVES

| | | Offspring | | | Expected | |
|---|---|---|---|---|---|---|
| Mate | Genotype | (C) Colored | (cc) White | Total | Colored | White |
| Daughter 253 | Cc | 18 | 5 | 23 | 17.3 | 5.7 |
| ½ sister 44 | Cc | 29 | 5 | 34 | 25.5 | 8.5 |
| Niece 199 | cc | 10 | 10 | 20 | 10.0 | 10.0 |
| Total | | 57 | 20 | 77 | 52.8 | 24.2 |
| Mother 8 | cc | 19 | 8 | 27 | 13.5 | 13.5 |
| Aunt 12 | cc | 17 | 8 | 25 | 12.5 | 12.5 |
| " 14 | cc | 2 | 1 | 3 | 1.5 | 1.5 |
| [2] Cousin 505 | cc | 9 | 5 | 14 | 7.0 | 7.0 |
| " 519 | cc | 1 | 2 | 3 | 1.5 | 1.5 |
| " 523 | cc | 10 | 8 | 18 | 9.0 | 9.0 |
| | | 58 | 32 | 90 | 45.0 | 45.0 |

In the first three matings there is a slight deficiency of whites, although not enough to require any explanation other than errors of sampling. In the matings of this male to his mother, two of her sisters and three cousins from the same pure stock, there appears a considerable departure from the expected ratio. The ratio obtained resembles a 2:1 ratio much more closely than a 1:1. In general, the white fowls are about half as numerous as should be expected if the difference between colored and white is determined by a single gene and if all combinations are equally viable.

In view of the evidence from normal ratios obtained in the $F_2$ generation and from other data as yet unpublished, it is certain that the white plumage of the fowls used is due to a single recessive gene. This is confirmed by the evidence and conclusions of Lippincott (1921), Sturtevant (1912) and Bateson (1902), who found what was presumably the same gene to act as a simple recessive to color. The explanation of the aberrant ratios obtained is more probably to be sought in a differential viability of the white and colored zygotes produced.

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[2] Pure White Wyandottes from same stock as mother of male 104.

If we suppose (1) that a lethal gene, l, determining the death before hatching of embryos homozygous for it ll to have been introduced by female 8, the mother of male 104; (2) that this gene is closely or completely linked with c, the gene for white plumage, and (3) that this lethal gene was present in other individuals of the stock from which female 8 came, then the results obtained may be satisfactorily explained.

On the assumption that female 8 is of the genotype ccLl and male 104 is CcLl then the zygotes produced by a cross between them should be

CcLL — colored
CcLl — colored
ccLl — white (viable)
ccll — white (dies)

The resulting ratio should be 2 colored: 1 white, and the ratio of 19 colored: 8 white actually obtained agrees well with this explanation. If the other pure White Wyandotte females from the same stock were of the same genotype, *i. e.*, ccLl, then, when crossed with the male carrying the lethal, their viable offspring should be colored and white in a ratio of 2: 1. The actual ratio of all offspring from the cross of CcLl male with ccLl females contrasted with the ratio expected on the above assumptions is as follows:

| | Colored | White |
|---|---|---|
| Actual | 58 | 32 |
| Expected | 60 | 30 |

The numbers involved are not large, but they are thought to afford a sufficiently close agreement with the numbers expected and to support the hypothesis proposed.

It is unfortunate that more sibs of the male which was tested could not be tested thoroughly for the presence of the supposed lethal gene. Three sisters when bred to this male produced one or more white chicks while two produced no whites. On the assumption of complete linkage between c and l, no white chicks would be produced if they carried the lethal, while, if free from the lethal, colored and white chicks should be produced in normal $F_2$ proportions. The numbers are not large enough to serve as a test and all sibs died before they could be mated again.

The colored daughter and half sister tested apparently did not carry the lethal since by this male they produced some white chicks. The white niece produced when bred to this male equal numbers of colored and white and probably did not carry the lethal.

In further support of the presence of the lethal may be cited: (1) An extremely high mortality of embryos early in incubation in the pure stock from which the lethal was presumably introduced (the average proportion of fertile eggs hatched in this stock was about 30 per cent.); (2) the high viability of embryos when this stock was crossed with the Pit Game, which supposedly lacked the lethal (the average proportion of fertile eggs hatched from this cross was 92 per cent.); (3) the low viability which resulted in the backcross of the lethal-bearing male to the pure Wyandotte stock (the proportion of fertile eggs hatched from this cross was about 20 per cent.). The factors responsible for mortality among embryos are too little known to place much emphasis on these latter indications; inbreeding is known to be one factor causing an increase in mortality of embryos, however, and it is probable that the segregation of lethal factors such as the one described is the primary cause of this result rather than that the inbreeding involved in producing the backcross chicks in this cross was the cause of the high mortality among embryos. (4) The mortality among the chicks hatched from crosses in which the lethal was supposedly involved was very high. It is possible that fowls heterozygous for the lethal are less viable than those which lack it entirely.

Some evidence indicates that the death of zygotes homozygous for the lethal occurs relatively early in incubation, since the ratio of colored to white chicks dying after the sixteenth day of incubation is very similar to the ratio among those actually hatched. It is hoped to secure more evidence on this point and to test the hypothesis more fully.

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# WHAT DID MAUPAS MEAN?

PROFESSOR GARY N. CALKINS
COLUMBIA UNIVERSITY

IN his fascinating little book on "Life and Death Heredity and Evolution in Unicellular Organisms," Jennings lays much stress on the conclusions which Maupas drew from his now classical experiments with isolation cultures of ciliate infusoria. Jennings uses these conclusions to support Weismann's and his own view that the primary effect of conjugation is to give rise to diverse stocks through inherited differences. In order to give effect to this interpretation he argues that in the majority of cases deterioration is probably due to faulty medium or methods and that natural death in ciliates amounts to infusoricide. "The real test lies in observing whether mating actually does remedy the degeneration. If it does not, the probability becomes strong that the degeneration is simply a pathological result of bad conditions. The evidence is becoming overwhelming that this is the case; that to avoid degeneration, it is merely necessary to avoid the bad conditions" (Jennings, 1921, p. 149). Furthermore, he holds that conjugation, except for the one case of *Uroleptus mobilis,* does not have any appreciable effect in restoring vitality as measured by the division rate, *i.e.,* it does not result in rejuvenescence.

Maupas provides ample evidence for this point of view in the two long papers which he published in 1888 and 1889, and an astute investigator would find little difficulty in digging it out. All that is needed really is patience. Jennings recognizes this and expresses it as follows: "It is because Maupas's papers, with their hundreds of pages of text filled with observational and experimental details, make hard reading, that it is possible for mistaken ideas of his results to become prevalent" (*l.c.,* p. 146). But even the astute investigator may trip up in the tangle of inconsistencies and contradictions which these pages contain. Maupas establishes such a tangle in connection with physiological deterioration which, as he states, occurs in all of the species cultivated by him. Thus on page 266 Maupas says: "In regard to Infusoria my cultures have demonstrated experimentally that these protozoa do not escape the general law of senescence. They use themselves up and grow old by the exercise of their functions, or in other words, because of a necessity inherent in their structure and constitution. The proof that the two halves resulting from any single bipartition are equivalent is evident from all my cultures, besides it has already been furnished definitely enough by Gruber's observations on the division of testate rhizopods. But that this equivalence is continued and constantly maintained without modification from generation to generation, that an individual after 50 or 100 bipartitions, for example, would be physiologically equal to the first progenitor, this is a conclusion against which I protest. If there are actually any monoplastids (Protozoa) in which such equivalence is indefinitely maintained we know nothing of them" (*l.c.*, p. 266 and 267).

This certainly is a very explicit statement and, indeed, this is the burden of his entire experimental work in proof of advancing age and senile degeneration in infusoria. But with this conception he introduced another which is not only inconsistent but is biologically untenable, *viz.*, the idea that with this deterioration the reproductive power by division remains intact and unaltered from beginning to end of the cycle. It is this latter idea which Jennings pounces on and uses with all the skill of a trained barrister. With evident satisfaction he quotes the following passage from Maupas' paper of 1889: "I have asserted, besides, that this power of multiplication is maintained regularly and uniformly during the entire life cycle; that there is no gradual weakening of this power from the first generation after conjugation up to the return of a new period of maturity. In other words, I deny that the infusoria after conjugation have a more energetic reproduction than they have at a later period'' (p. 504). Let me add another citation from the earlier 1888 paper which adds fuel to Jennings's fire: After stating his conception of physiological usury he adds: ''The power of multiplication follows no such diminishing and parallel course. It is maintained almost intact even a long time after the other functions, and the entire organism, are shown to be greatly reduced by senile degeneration. We have seen, in short, during the well-advanced stages of our cultures that the infusoria, although feeble and much reduced in size, continue to divide with almost the same rapidity as at the beginning'' (1888, p. 273).

It is difficult to see how all the physiological activities of a ciliate can be gradually reduced and ultimately worn out without involving any change in the rate of multiplication by division. On this hypothesis, with loss of the powers of locomotion, food taking and digestion, growth of the daughter cells must be impaired and a next division must take place in an individual of reduced size. If this continues through 316 to 319 generations at the same division rate the ultimate products of division must be very small indeed. If physiological usury were taking place, an increasingly longer interval between successive divisions would be necessary. That such was the case in some at least of Maupas's cultures is shown by the following quotation which flatly contradicts the generalization quoted above: ''In cultures begun on May 1st more than one division in twenty-four hours was no longer maintained during the months of September and October. In November and December the divisions succeeded one another at intervals of two, three and four days, and in January they were reduced to three divisions in twenty-six days'' (1888, p 217). The inconsistency leads to scepticism over his results which may be expressed either in doubt as to the actual occurrence of physiological deterioration, or in doubt as to the invariability of the division rate.

As a matter of record Maupas hangs himself on one of the horns of the dilemma and shows by his own data that his conclusion regarding a uniform division rate for all of his cultures was incorrect. He maintained six different cultures to the end in each case, and the forms used were (1) *Stylonychia pustulata* (215 generations); (2) *Stylonychia pustulata* from an ex-conjugant (316 generations); (3) *Stylonychia mytilus* (319 generations); (4) *Onychodromus grandis* (320–330 generations); (5) *Oxytricha sp.* (320–340 generations), and (6) *Leucophrys patula* (660 generations). In at least two of these (numbers 5 and 6) the number of generations was obtained by computation on the basis of the daily temperature, a procedure which does not inspire confidence in the exactness of Maupas' methods. In connection with *Leucophrys patula* he states: "En tenant compte de la température des mois pendant lesquels cette culture a duré et de la puissance de multiplications des individus ainsi cultivées, j'ai calculé que le nombre total des générations devait attendre le chiffre de 660 au minimum au moment de l'extinction" (1888, p. 242). Again in connection with *Oxytricha sp.*: "En calculant le nombre des générations, d'apres la température des mois pendant lesquels cette culture a duré et proportionnellement a cette puissance de multiplication, j'arrive a un total approximatif de 320 à 340" (*l.c.*, p. 223).

It is unfortunate that Maupas did not see fit to publish the full records of his six cultures. Computation of divisions on the basis of the average temperature gives a result which can not be accepted, for it begs the question of decreasing vitality and multiplication. Two of his cultures must therefore be eliminated and probably a third, since he was uncertain of the length of life of *Onychodromus grandis* (320–330 generations). This leaves only three cultures from which a legitimate conclusion of an equal and continuous division rate throughout the life cycle could be drawn. For only one of these (number 2) does he give the daily records of number of individuals, number of divisions and temperatures. "I shall not reproduce here," he says, "the daily observations of all of these species. Their detailed presentation would lead me to fastidious and uninteresting repetitions. I shall be content with giving as a specimen the longest and most complete culture which I have made. It will suffice to furnish an idea of the others" (1888, p. 196). From the various citations given above it is evident that he thought he had found that in none of his cultures was there a decrease with age, in the division rate.

It is quite evident, however, that Maupas based his generalization upon the one culture the records for which he gives in full, namely, his culture of *Stylonychia pustulata* (number 2). These records must have been constantly before him when his 1888 paper was compiled, and these must have been the only results remembered when his 1889 paper was written. They certainly bear him out. From his daily records for this culture on pages 197 to 201 it is possible to work out the average division rate for 10-day periods for the lifetime of the culture. The average temperatures for such periods can be easily computed also from the same table. These on plotting give the curve of vitality shown in Diagram 1. Making allowance for the differences in temperature it is easily seen where Maupas got the basis for his conclusion that the division rate remains practically intact from beginning to end.

Generalizations, however, are notably unsafe, particularly if they do not rest on the complete digestion of a mass of data such as Maupas must have accumulated. It is evident that he did not give equal weight to all of his records, nor is there excuse for his oversight of pertinent data which he presents in connection with another matter. He attempted to work out the approximate period in the life history of *Stylonychia mytilus* at which the micronuclei disappear. Now the disappearance of the micronuclei is not a matter which interests us here, but the data used to furnish the exact age in days and generations of the individuals studied provides all the material necessary for a history of the division rate from beginning to end of the culture. This is all summarized in his 1888 paper on pages 213 and 214. The culture was started on May 1, 1886, with one individual and lasted until January 26, 1887, when the last individual died in the 319th generation. The data which he thus gives us and the material for constructing a curve of vitality on the basis of 10-day division rates are condensed in the following table:

DIAGRAM 1

**Stylonychia pustulata**

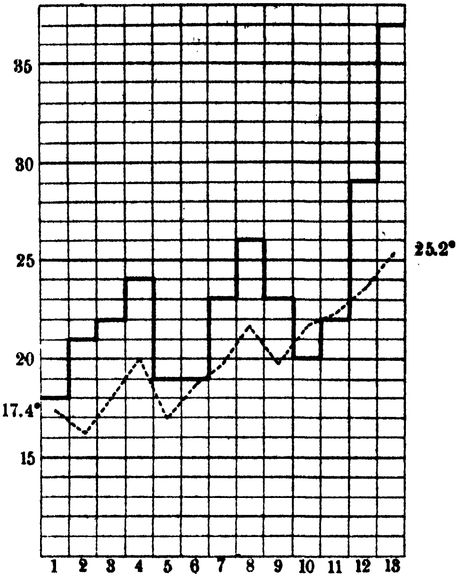

DIAGRAM 1. Generations by division of *Stylonychia pustulata* averaged for 10-day periods. From Maupas' records on pages 197–201 of his 1888 paper. The average temperatures for the same 10-day periods are shown in the dotted line curve.

July 16 in the 148th generation (*i.e.*, 76 days from May 1st)
Aug. 15 in the 210th generation (*i.e.*, 30 days from July 16)
Sept. 14 in the 250th generation (*i.e.*, 30 days from Aug. 15)
Sept. 29 in the 261st generation (*i.e.*, 15 days from Sept. 14)

Oct. 14 in the 277th generation (*i.e.*, 15 days from Sept. 29)
Nov. 2 in the 294th generation (*i.e.*, 19 days from Oct. 14)
[1] Nov. 23 in the 305th generation (*i.e.*, 21 days from Nov. 2)
Dec. 6 in the 310th generation (*i.e.*, 13 days from Nov. 23)
Jan. 26 in the 319th generation (dead) (*i.e.*, 50 days from Dec. 6)

The full life history curve of this culture based upon the following table from these data is given in Diagram 2:

| Periods | Days | Divisions | Daily Div. Rate | 10-day Div. Rate | No. of 10-day Per. |
|---|---|---|---|---|---|
| From May 1 to July 16 | 76 | = 148 | 1.94 | 19.4 | 7 3/5 |
| " July 16 to Aug. 15 | 30 | 210 — 148 = 62 | 2.06 | 20.6 | 3 |
| " Aug. 15 to Sep. 14 | 30 | 250 — 210 = 40 | 1.33 | 13.3 | 3 |
| " Sep. 14 to Sep. 29 | 15 | 261 — 250 = 11 | .73 | 7.3 | 1 1/2 |
| " Sep. 29 to Oct. 14 | 15 | 277 — 261 = 16 | 1.07 | 10.7 | 1 1/2 |
| " Oct. 14 to Nov. 2 | 19 | 294 — 277 = 17 | .89 | 8.9 | 2 |
| " Nov. 2 to Nov. 23 | 21 | 305 — 294 = 11 | .52 | 5.2 | 2 |
| " Nov. 23 to Dec. 6 | 13 | 310 — 305 = 5 | .38 | 1.8 | 1 |
| " Dec. 6 to Jan. 26 | 50 | 319 — 310 = 9 | .18 | 3.8 | 5 |

DIAGRAM 2

**Stylonychia mytilus**

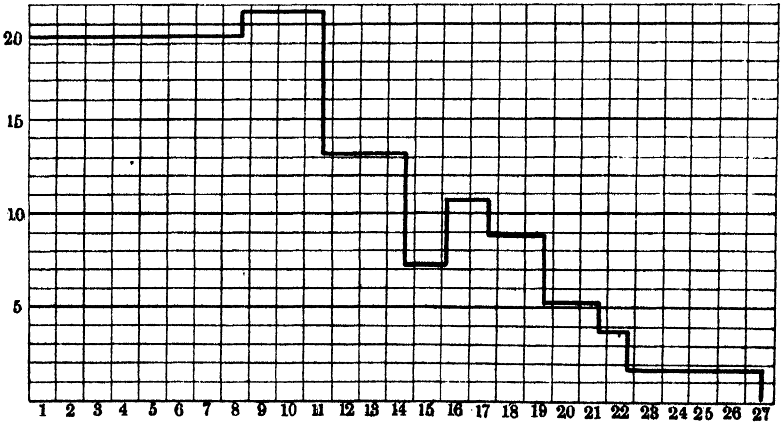

DIAGRAM 2. Generations by division of *Stylonychia mytilus* averaged for 10-day periods. From data on pages 213 and 214 of his 1888 paper.

In both diagrams the ordinates represent the number of divisions, the abscissas the consecutive 10-day periods.

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[1] Maupas interpellates another date and record between November 2 and November 23 which is obviously a typographical error. After November 2 his next record is "November 28 (301st generation)," he then continues with "November 23rd (305th generation)." I have used the November 23rd record as covering and including his record labelled November 28.

This is one of three cultures of *S. mytilus,* but the only one in which he kept a daily record. All three cultures, however, "behaved in an absolutely uniform manner (Elles se sont, d'ailleurs, comportées toutes trois d'une façon absolument uniforme)" (p. 212).

Here, then, is a curve of vitality constructed from Maupas's own data which, there is no reason to doubt, are as accurate as the data for *S. pustulata.* Does this curve justify his generalization that the data for *S. pustulata* are of the same type as for all the other cultures? Does this curve justify the conclusion that the division rate remains practically the same from beginning to end? Does it support the contention that the power of multiplication is neither decreased before nor increased after conjugation? Does it give him a basis for the statement: "I deny that the infusoria after conjugation have a more energetic reproduction than they have at a later period" (1889, p. 504)? Emphatically it does not.

What did Maupas mean? The inconsistencies and contradictions have led his successors to opposite points of view. Half of Maupas's published data support one side, half support the other. Jennings is correct so far as his particular half is concerned: "Expert biologists" and "investigators as experienced as Woodruff and Erdmann" (Jennings, p. 145, footnote) were right as far as the other half was concerned. Apparently, so far as Maupas's results are to be accepted, the matter stands 50–50. This is only apparent, however, for not only does he contradict himself, but in the light of subsequent culture experiments with hypothrichous ciliates, the vitality curve for *S. pustulata* above has never been duplicated, while all later life cycles, based on better technique and more careful methods, agree with the second curve above, which we have constructed for *S. mytilus.* Thus Woodruff's (1905) curves for *Oxytricha fallax, Pleurotricha lanceolata,* and *Gastrostyla steinii* are exactly of the type which I have drawn from Maupas's data for *S. mytilus,* while the latter curve might be substituted without fear of detection, for a typical life cycle of *Uroleptus mobilis.* Indeed, the evidence is to-day overwhelming that vitality as measured by the division rate of infusoria gradually decreases with age.

Let us now consider a second point which Jennings makes in connection with the division rate subsequent to conjugation as a test of rejuvenescence. Here again his main support is derived from "that greatest of investigators of the Protozoa, Émile Maupas" (Jennings, *l.c.*, p. 64). We have given enough, however, to show what was the nature of that support. Some other experiments of Maupas bearing on this point will be mentioned later. A second great name which Jennings draws over to his own side of the argument is that of Richard Hertwig. "It is not generally realized that the work of Maupas and of Richard Hertwig, on whose authority the theories of rejuvenescence by conjugation largely rest, was squarely opposed to the idea that this rejuvenescence manifests itself by an increase of reproductive vigor. It is worth while to emphasize this point, for upon it an extraordinary error has become widespread even among expert biologists."

"Maupas rejected emphatically the idea that aging shows itself in a decrease of the rate of reproduction and that conjugation restores this declining rate. He asserted positively that no such decline occurred before conjugation and that after conjugation reproduction was not more rapid than before, and he based these statements on the results of careful experimentation. Richard Hertwig's experiments led to the same result and induced him to subscribe completely to Maupas's assertions on this point. The matter is important, since the doctrine that conjugation restores the declining fission rate depends largely on their supposed support of it" (Jennings, *l.c.*, pp. 144 and 145).

Maupas and Hertwig, therefore, should be considered together in this matter of rejuvenescence, since the theory "depends largely on their supposed support of it." Let us first see just what Hertwig's contribution was.

In an earlier paper Jennings was not quite so happy over Hertwig's support on this problem: "He (Hertwig) gives only a general account of his experiment, not even mentioning the number of cases examined but some cultures obtained from split pairs were kept as long as three months" (Jennings, 1913, p. 358). The full extent of Hertwig's original work is expressed in the following quotation from his paper of 1889: "In order to have complete assurance on this point (division rate after conjugation) further culture records which I have had no time as yet to make, should be at hand; but I have made a very simple experiment which safely shows that conjugation-hungry infusoria maintain an intact, or as I believe, even an increased division activity, indicating a conclusion opposite to that of Bütschli and Engelmann. I have separated individuals of Paramecium which were swimming about in pairs and have cultivated them separately. For greater sureness I have separated individuals already united and within the hour of fusion and have cultivated them separately in hollow slides with nutrient media. Some of these I used in order to determine any changes during the first 24 hours but observed nothing worthy of remark; others I have maintained in culture for weeks and months. One such (*nicht einmal mit besondere Sorgfalt geführte Kultur*) lasted over three months from the end of March to the beginning of July. As a first result I noted a striking activity in divisions in animals prevented from conjugation. Although my experiments are not conclusive I may state that these artificially separated animals divide for a long time more energetically than exconjugants. In the first five days and making allowance for the period of nuclear reconstruction of the exconjugants, nearly twice as many individuals were formed" (1889, p. 222). It is hardly necessary to point out that "twice as many individuals" would mean just one more division!

The above citation includes all the experimental data and records and the sole original observations made by Hertwig, and these constitute the support which Jennings gets from him. But: "Richard Hertwig (1889) found in his experiment, to his surprise (as will any one that tries it), not only that Paramecia which had conjugated did not reproduce faster, but that, on the contrary, it was those that had not been allowed to conjugate that multiplied more rapidly" (Jennings, *l.c.,* p. 146). One swallow does not make a drink and one experiment, incomplete at that, does not give basis for a generalization. As a matter of fact, Hertwig's position in the matter was apparently based mainly on Maupas's results. His "not once with an especially carefully conducted culture" (see German above) gives his situation away. Nevertheless, Hertwig was led to say: "The grounds on which this theory is based have already been combated by Maupas; he showed by extended experiment that the power of multiplication of an infusorian is neither decreased before conjugation nor increased after it. . . . I am compelled to say that Maupas was entirely right" (quoted from Jennings, 1921, p. 147).

Let us see what further evidence, beyond the one culture of *Stylonychia pustulata* examined above, Maupas adduced in support of the conclusion that multiplication is "neither decreased before conjugation nor increased after it." On page 255 Maupas states: "I was not satisfied with this single experiment. I isolated other exconjugants of *Stylonychia pustulata,* also of *Onychodromus grandis,* of *Euplotes patella, Paramecium aurelia* and of *Leucophrys patula.* I followed, day by day, the successive generations of their descendants for periods varying from 15 days to one or two months. In none of these species have I noted the least difference in the succession of bipartitions. All of the individuals behaved in the same manner regardless of any recent or remote conjugation" (1888, p. 255). Here is another general statement without accompanying data, while the scepticism raised by the discrepancy between his conclusion and his published data for the two species of Stylonychia makes one doubt the validity of this one. We are not informed as to whether his data were obtained from actual records or were computed on the basis of the temperature; also fifteen days to two months is too short a period for safe conclusions even with careful methods. In no case furthermore does he compare the division rate of the offspring with that of the parent stock for the same periods. Had he done so he would have reached a different conclusion.

Jennings apparently in 1921 is still reluctant to give up the opinion which he expressed in 1913, as follows: "But the facts appear to be clear, so far as the infusoria go. In view of the large number (*sic*) of experiments made by Maupas on this point, the absolute agreement (*sic*) of his results with those of Richard Hertwig; the fact that these men are perhaps the most thorough investigators that have ever worked along these lines; the further fact that there exist no careful experimental results opposed to these; and finally the very large body of evidence presented in the present paper, all giving the same results—is it not time that the statements or implications that in the infusoria conjugation results in increased reproduction should disappear from the literature of Science?" The fancied support which Jennings claims from these noted investigators turns out to be very questionable.

Now let us examine the evidence which Jennings himself brings to bear on the problem, evidence which, with the foregoing, he believes is enough to warrant the disappearance of further reference to rejuvenescence (increased reproduction after conjugation) in the literature of science. This evidence appears in a number of papers published by Jennings from 1908 to 1916 and is summarized in his book of 1921. The admirable thoroughness, the mastery of technique, and the skillful marshal-ing of a wealth of data which he gives in full, together with his persuasive manner of presentation, place him immeasurably above these others whose support he claims. Indeed the only serious opponent of rejuvenescence by conjugation in ciliates is H. S. Jennings.

Unfortunately, all of Jennings's experiments, like Hertwig's, were made with, and his conclusions were drawn from one ciliate—Paramecium. Unfortunate because all conclusions as to the division rate before and after conjugation and based on experiments prior to 1914 are nullified by the discovery of monthly parthenogenesis (endomixis) made by Woodruff and Erdmann in that year. The conclusions of Hertwig (1889), of Calkins (1902–4) and of Jennings (1908–13) in regard to rejuvenescence in Paramecium are affected by this discovery, as was clearly demonstrated by Erdmann in 1919 and by Hartmann in 1921. The only exceptions allowable are those based upon observations made on the division rate in inter-endomictic periods. Of these allowable cases Jennings' paper of 1913 contains a great many, for the division rate for 11–20 days of exconjugants is contrasted with the division rate of individuals of the same age and ancestry, which were separated at the beginning of conjugation ("split" pairs). In many repeated experiments his results were uniform and his conclusion that conjugation causes a *decrease* in the division rate appears on the surface to be justified.

Another interpretation of these results, however, is possible. One result on which he laid emphasis was the invariably higher death rate and higher percentage of abnormalities of ex-conjugants as compared with non-conjugants under identical environmental conditions, a death rate amounting in one experiment to from 38 per cent. to 59 per cent. of the ex-conjugants. This he interpreted as due to "incompatible combinations" in amphimixis and as illustrating variation brought about by conjugation (1913, p. 361).

This higher death rate is significant and affects the interpretation of all of the results obtained by Jennings. Why should conjugation result in such a death rate for Paramecium when in *Uroleptus mobilis* cultivated for the last six years the death rate for ex-conjugants has been negligible, never amounting to more than three per cent.? If variation is responsible in one case there is reason to expect a like variation in the other. Variation through amphimixis is not a satisfactory explanation of the difference. Nor does it afford any explanation of the 100 per cent. of ex-conjugant mortality obtained by Bütschli with *Blepharisma lateritia;* nor of the 100 per cent. mortality obtained by Baitsell (1912) with *Stylonychia pustulata* and by Calkins (1912) with *Blepharisma undulans.* Mortality similar to that found by Jennings was also obtained by Calkins (1904) for *Paramecium caudatum.* Here the death rate of ex-conjugants from "wild" (pond) cultures amounted to from 20 per cent. to 30 per cent., but in material from prolonged laboratory cultures it rose to 94 per cent. On what basis of reasoning can we hold that incompatible combinations cause a mortality of 94 per cent. in laboratory material and only 30 per cent. in material fresh from pond water? Such cases make it very difficult to believe that variations brought about by amphimixis are responsible for the death rate. It is much more probable that appropriate environmental conditions have not been provided for the organisms during a critical period of reorganization and early development. A "standard hay infusion" was perfectly satisfactory as a culture medium for the vegetative life of *Blepharisma undulans* or for *Stylonychia pustulata,* but ex-conjugants invariably died in it. It, therefore, was an imperfect medium for these organisms, since something was lacking in it to safeguard them during a critical period. In the medium used for *Uroleptus mobilis* on the other hand, practically every ex-conjugant continues to live, if allowed to, hence it may be regarded as a perfect culture medium for Uroleptus. Jennings apparently takes it for granted that the standard hay infusion is the most perfect medium obtainable for Paramecium since it is suitable for the ordinary vegetative life, and he does not consider it as a possible factor in connection with the high mortality of ex-conjugants. It must be considered, however, and, in my opinion, it is a more probable cause of mortality than are "incompatible combinations."

"In Paramecium not only do those that have conjugated multiply less rapidly than before, but a great many of them die after conjugation—although without conjugation they live vigorously. Many others are weak and sickly, multiplying but little. Still further, conjugation produces a great number of abnormalities and monstrosities, such as do not occur without mating" (Jennings, 1921, p. 150). How does this bear on the fact of the decreased division rates, as found by Hertwig and Jennings for ex-conjugants? Jennings provides the application: "The grounds just set forth as possibly accounting for the greater death rate of the ex-conjugants perhaps play a part also in the production of abnormalities" (p. 361, 1913). The same causes which produce a high mortality might be expected to produce abnormalities and this would follow from reduced vitality due to imperfect cultural conditions during the critical period. Pursuing the argument a step farther, the same causes may be regarded as being responsible for the reduced division rate of ex-conjugants as compared with non-conjugants.

Certainly no such results have been obtained in my studies on *Uroleptus mobilis.* Here there is no question of the suitability of the medium, and there is an invariable increase in the division rate of the ex-conjugants over the non-conjugants. Furthermore, there is the same degree or extent of increase after conjugation in my cultures to-day as there was at the outset, and this after nearly six years of cultivation in an invariable culture medium.

In the following table each "series" represents the progeny of an ex-conjugant, the division rate of which is the average division rate of five pure lines started from the first five individuals derived from an ex-conjugant. From my 103 different series up to the present, all obtained by conjugation or by parthenogenesis from pedigreed lines, and all derived from the same single ancestral cell isolated on November 27, 1917, I have selected four groups of five successive series each, from the records for different years and chosen practically at random.

It will be noted that the extent of rejuvenescence, shown by the difference between the 60-day division rates of parent and offspring, is highly variable. It amounts to only one division per 10-days in couplet 3; to one and a half divisions in 10-days in couplets 1 and 15 but rises to a difference of 13.1 and 11.9 in couplets 7 and 14. As I have previously shown (1920), this variability is correlated with the age of the parents at the time of conjugation. Much more striking evidence of this might be selected from my records, but these are significant as random samples.

The correlation of parents' age and the extent of rejuvenescence is important in determining the significance of post-conjugation division rates. Diagram 3 shows a composite curve of vitality of the first twelve series of Uroleptus and a curve (dotted line) indicating the ideal extent of rejuvenescence in ex-conjugants at all periods. We would not attach much importance to a difference between parent and offspring of only one division in 10 days, while for a period of the first 20 days it is not an infrequent occurrence for the division rate of the offspring to fall below that of the parent. Thus in couplet number 1 the division rate of the parent for the first 20 days of the offspring's life was 19.4 per 10-days, while the rate of the offspring was 18.7; or in couplet number 3 the rate for the parent was 14.9, while that for

### DIVISION RATES OF 20 COUPLETS OF OFFSPRING AND PARENTS TAKEN AT RANDOM FROM FOUR DIFFERENT YEARS OF RECORDS FOR UROLEPTUS MOBILIS

| | | 1st 10-days | 2d 10-days | 3d 10-days | 4th 10-days | 5th 10-days | 6th 10-days | Average rate 1st 60 days | Age of Parent |
|---|---|---|---|---|---|---|---|---|---|
| 1 | Series No. 2 | 18.6 | 18.8 | 16.2 | 16.8 | 17.2 | 15.6 | 17.2 | |
| | Parent No. 1 | 20.8 | 18.0 | 12.6 | 13.2 | 14.8 | 14.6 | 15.7 | 78 gen. |
| 2 | Series No. 3 | 16.0 | 18.2 | 16.0 | 17.0 | 17.6 | 18.4 | 17.2 | |
| | Parent No. 1 | 13.2 | 14.8 | 14.6 | 13.2 | 15.0 | 13.6 | 14.9 | 137 |
| 3 | Series No. 4 | 13.4 | 13.8 | 16.4 | 19.8 | 20.2 | 19.6 | 17.2 | |
| | Parent No. 2 | 15.6 | 14.2 | 16.4 | 15.6 | 17.4 | 18.0 | 16.2 | 86 |
| 4 | Series No. 5 | 17.4 | 19.4 | 21.0 | 19.6 | 15.6 | 15.8 | 18.1 | |
| | Parent B | 14.4 | 13.8 | 13.6 | 15.0 | 12.2 | 4.0 | 12.1 | 115 |
| 5 | Series No. 6 | 19.6 | 16.8 | 17.8 | 15.8 | 14.8 | 16.0 | 16.8 | |
| | Parent No. 1 | 12.8 | 7.4 | 11.0 | 7.0 | 9.0 | 7.6 | 9.1 | 237 |
| 6 | Series No. 15 | 19.6 | 13.8 | 14.0 | 12.8 | 14.0 | 9.4 | 13.9 | |
| | Parent No. 8 | 3.6 | 0.8 | 0.2 | 0.4 | 0.2 | 0.0 | 0.8 | 245 |
| 7 | Series No. 16 | 9.0 | 14.0 | 13.3 | 13.6 | 13.6 | 12.6 | 12.7 | |
| | Parent No. 9 | 5.4 | 10.0 | 10.4 | 7.6 | 5.6 | 2.6 | 6.9 | 208 |
| 8 | Series No. 17 | 8.5 | 14.0 | 13.5 | 14.5 | 13.5 | 13.0 | 12.8 | |
| | Parent No. 9 | 5.4 | 10.0 | 10.4 | 7.6 | 5.6 | 2.6 | 6.9 | 208 |
| 9 | Series No. 18 | 13.8 | 16.0 | 13.8 | 14.6 | 18.2 | 16.8 | 15.5 | |
| | Parent No. 13 | 13.6 | 12.8 | 13.2 | 10.0 | 12.4 | 12.2 | 12.3 | 120 |
| 10 | Series No. 19 | 14.0 | 10.8 | 7.6 | 11.2 | 7.8 | 10.8 | 10.4 | |
| | Parent No. 11 | 6.6 | 3.0 | 0.6 | 0.0 | 0.0 | 0.0 | 1.7 | 225 |
| 11 | Series No. 60 | 16.0 | 17.0 | 18.0 | 17.0 | 15.0 | 16.0 | 16.5 | |
| | Parent No. 59 | 14.4 | 15.6 | 15.2 | 12.6 | 14.6 | 13.6 | 14.3 | 51 |
| 12 | Series No. 61 | 17.2 | 17.0 | 16.2 | 15.8 | 15.6 | 13.8 | 15.9 | |
| | Parent No. 59 | 14.6 | 13.6 | 11.8 | 10.4 | 8.6 | 8.4 | 11.2 | 104 |
| 13 | Series No. 62 | 12.8 | 13.8 | 13.6 | 14.2 | 13.6 | 13.2 | 13.5 | |
| | Parent No. 60 | 11.0 | 14.0 | 12.8 | 11.6 | 9.4 | 7.8 | 11.1 | 97 |
| 14 | Series No. 63 | 14.2 | 15.0 | 13.4 | 14.2 | 13.0 | 12.8 | 13.8 | |
| | Parent No. 56 | 2.6 | 3.4 | 2.8 | 2.2 | .6 | 0.0 | 1.9 | 170 |
| 15 | Series No. 64 | 15.2 | 15.4 | 14.4 | 11.4 | 12.4 | 13.0 | 13.6 | |
| | Parent No. 61 | 13.8 | 14.4 | 12.4 | 11.0 | 10.8 | 10.4 | 12.1 | 74 |
| 16 | Series No. 90 | 13.2 | 15.2 | 17.8 | 15.4 | 14.0 | 16.2 | 15.3 | |
| | Parent No. 87 | 11.4 | 12.8 | 14.4 | 13.8 | 12.0 | 11.8 | 12.7 | 88 |
| 17 | Series No. 91 | 12.0 | 16.2 | 17.9 | 14.6 | 16.2 | 16.0 | 15.5 | |
| | Parent No. 89 | 11.2 | 11.6 | 12.0 | 11.6 | 11.6 | 11.0 | 13.0 | 30 |
| 18 | Series No. 92 | 17.6 | 14.4 | 13.8 | 13.6 | 19.0 | 17.6 | 16.0 | |
| | Parent No. 91 | 16.0 | 12.8 | 13.4 | 11.0 | 15.2 | 13.8 | 13.7 | 52 |
| 19 | Series No. 93 | 17.4 | 14.4 | 15.0 | 12.8 | 18.2 | 17.0 | 15.8 | |
| | Parent No. 91 | 16.0 | 12.8 | 13.4 | 11.0 | 15.2 | 13.8 | 13.7 | 70 |
| 20 | Series No. 94 | 13.2 | 11.2 | 10.6 | 16.4 | 15.8 | 14.6 | 13.3 | |
| | Parent No. 88 | 11.2 | 11.4 | 8.6 | 11.2 | 10.6 | 11.6 | 10.7 | 149 |

the offspring was only 13.6. But for the 60-day period the difference was reversed in both cases. In both of these cases the parents were in full vitality at the time of conjugation and no such approximation in rates will be found in cases where the parents were of advanced age at the time of conjugation. The age in generations of the parents at the time of conjugation is given in the last column of the table. It will be seen that as age increases the division rate of the parent does not approach at any period that of its filial series. Now if this is true for Uroleptus it may be equally true for Paramecium, where by virtue of the frequency of parthenogenetic periods, the parents are apparently always young. This, therefore, may be another factor to be considered in the interpretation of Jennings's results where the division rate of the offspring for a period of 21 days was sometimes less, sometimes the same as, and sometimes more than that of the parent. Because of the shortness of the

DIAGRAM 3

Uroleptus mobilis
Composite Curve of Vitality of 1st 12 Series.

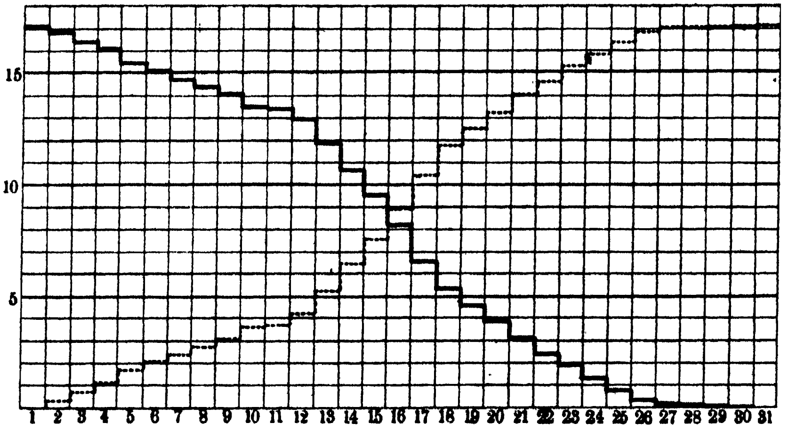

DIAGRAM 3. Composite curve of vitality of the first 12 series of *Uroleptus mobilis* by 10-day periods. The ideal expected rejuvenescence from conjugation at any period is indicated by the dotted curve.

inter-endomictic period in Paramecium the vitality of parent and offspring can not be compared for more than two full 10-day periods. Neither Maupas nor Hertwig nor Jennings has furnished comparative records of parent and offspring for a longer period than 21 days.

It appears, therefore, that Jennings' recommendation to eliminate the idea of rejuvenescence from the literature of science rests on a very weak basis indeed. The support he seeks from his predecessors has failed him; the data and conclusions of Maupas are shown to be inconsistent and contradictory; those of Hertwig incomplete and inconclusive. His own experiments, so carefully planned and executed, were made on one of the most unfavorable and most unrepresentative types of organism that could have been chosen from the common ciliates. His conclusions from these experiments in respect to some of the fundamental matters in biology—rejuvenescence, heredity and variations—must remain unproved until no question can be raised as to whether culture medium, or vitality of parent, or amphimixis was responsible for the variations observed.

This criticism applies mainly to the conception of variations in vitality as adduced in proof that rejuvenescence, in the sense of increased reproduction, is not a result of conjugation. I have no quarrel with those who insist on amphimixis as a possible source of variation; the division rate indeed may be indirectly subject to such variations, but in my opinion this has never yet been proved. There is abundant evidence of variations in my records and data on *Uroleptus mobilis* which I shall analyze in the near future. One such variation is indicated in the table given above. The first quintet of couplets shows an average division rate for the first 60 days of the offspring of more than 17 divisions per 10-days for all series from young parents. The fourth quintet, made up chiefly of series from young parents, shows an average division rate of approximately only 15 divisions per 10-days for the first 60-days. Neither this variation nor any other which I have observed shows any evidence that variations are developed in any such sudden way as Jennings maintains for Paramecium.

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# SHORTER ARTICLES AND DISCUSSION

## THE SUBCOSTAL VEIN IN THE WINGS OF INSECTS[1]

THE students of the wings of insects are apparently all agreed that the primitive subcosta was a two-branched vein. While there is unanimity of opinion as to the structure of this vein, there has been the greatest difference as to the way in which the two parts have been homologized or even recognized by these same students. Subcosta only rarely exists in its simplest condition, a long stem with two branches each continuing independently to and terminating in the costal margin. Such a condition is found in the wings of Hepialus, Mnemonica, Sthenopsis and Rhyacophila.

The two branches of subcosta may be modified in different ways, but whatever the line of modification there is left an unbranched vein extending from the proximal end of the wing to the margin. This unbranched vein, regardless of its origin or homology, is generally labelled as subcosta, Sc. While in the orders with accessory veins, the branches of subcosta can not be identified with certainty, yet in those wings where the accessory veins are wanting, there should be no such difficulty.

The great majority of lepidopterous wings have subcosta represented by a single unbranched vein and this vein is generally labelled as Sc. From a study of pupal and adult wings of Hepialus it has been shown that so far as this family is concerned it is always the first branch of subcosta, subcosta-one, that atrophies. The evidence for this family is conclusive whether drawn from the pupal wings, where there is a decided weakening of the tracheæ of subcosta-one, or from the adult where some individuals of the same species may have subcosta-one present in the wings of one side and wanting in the wings of the other or present in one wing of one side and wanting in the other wing of the same side. In those Hepialidæ where subcosta is unbranched, this vein is correctly labelled only as subcosta-two and never as Sc. The characteristic form and position of the subcostal vein in the Frenatæ leaves no doubt but that this vein also should be labelled as subcosta-two. In the Lepidoptera subcosta is, therefore, modified by the atrophy of subcosta-one, and the labelling of subcosta and the subcostal cells should show this condition.

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[1] Contributions from the Entomological Laboratories of the University of Illinois No. 76.

Another characteristic way in which subcosta and its branches are modified is shown by the wings of certain stone-flies, as Nemoura and Tæniopteryx. In such wings subcosta-one extends directly to the wing margin as in the primitive type while the intermediate part of subcosta-two is anastomosed with radius-one. There is a free part of subcosta-two before this anastomosis and another part beyond it which terminates in the wing-margin. This condition undoubtedly arose from the migration of subcosta-two toward radius-one until the two came into contact. There thus resulted a fusion of the two veins at one point. Since the anastomosis of subcosta-two and radius-one offers a more efficient system of bracing of the costal margin, this undoubtedly led to a continuation of the anastomosis on each side of the original point of contact, together with a straightening of the two free parts of subcosta-two, approximating closer and closer to a perpendicular condition as the anastomosis proceeded. This produced in the end the type of subcosta found in the genera of stone-flies named. This is apparently the most common way in which subcosta is modified.

The wings of stone-flies illustrate a primitive condition, but in the wings of most insects where this type of modification can be identified, the anastomosis has proceeded much farther. The proximal free part of subcosta-two, the portion connected with subcosta-one, has continued to combine with radius-one until it is an oblique or perpendicular transverse vein extending between subcosta-one and radius-one. Such a condition as this is found in the wings of the Mecoptera, Panorpa and Bittacus, and in the wings of the generalized Hymenoptera. In this latter order the parts of subcosta-one, the proximal free part of subcosta-two, the portion of subcosta-two anastomosed with radius-one, and the distal free part of subcosta-two can be readily identified in the front wings of such generalized saw-flies as those of the genera Itycorsia and Macroxyela. The hymenopterous type of subcosta, the condition found in the great majority of the species of this order, has arisen from the fusion of the stem of subcosta with that of radius, eliminating the proximal free part of subcosta-two, while subcosta-one forms a short transverse vein, cross-vein-like, extending from the fused subcosta-two and radius. This cross-vein-like structure is found only in the saw-flies and soon disappears so that only the free part of subcosta-two is left, the short distal free portion terminating in the margin of the wing and forming the proximal end of the stigma.

A later stage in the modification of subcosta is the complete fusion of the distal free part of subcosta-two with radius-one. This is the condition characteristic of all Diptera. The simplest form of subcosta in this order is found in the wings of the Tanyderidæ, as Protoplasa and Tanyderus, and the Tipulidæ, as Limnobia, Dicranomyia, and a host of other genera. The general appearance of subcosta is only a slight change from that of the hymenopterous genera Macroxyela, Odontophyes, and Megaxyela, where the distal free part of subcosta-two is very short. The cross-vein-like proximal portion of subcosta-two, called the subcostal cross-vein by older authors, is very rarely absent in the families named. This condition has been identified by dipterologists in isolated genera of other families of Nematocerous Diptera. While subcosta-one has generally been correctly labelled in the wings of these and the free part of subcosta-two has been a few times labelled as subcosta-two, no writer on the Diptera or on the wings of insects has given the vein behind subcosta-one its proper designation, subcosta-two plus radius-one. The subcostal part of the label has always been ignored. The wings of the species of Conops, a genus widely separated from all those just named, has a cross-vein-like structure located near the tip of subcosta-one. A similar condition is found in the wings of Zodion and Stylogaster, other genera of Conopidæ. That such widely separated genera should have similar structures in the subcostal region has excited my interest for several years. No one apparently has mistrusted, judging at least from published results, that any of the intervening genera between Conops and the Tipulidæ had retained any indication of the cross-vein-like proximal transverse part of subcosta-two. Instead of its being the exception that this free part of subcosta-two is preserved, it is in reality more exceptional to find this vein wanting. It is the rule, therefore, to have subcosta branched in the Diptera and not a single vein.

The subcostal fold and the migration of the free part of subcosta-two far toward the proximal end of the wing, together with the fact that no one apparently has looked for it, accounts for the free part of subcosta-two not having been found. This vein may occur anywhere between the tip of subcosta-one and the humeral cross-vein, frequently nearer the cross-vein and often in line with it. There is for instance a distinct free part of subcosta-two in Midas, Hilaria, Docosia, Tabanus, Rhyphus, Hesperinus, Culex, Dixa, Leptis, Erax and Calliphora. The transverse thickening in the stem of radius opposite the humeral cross-vein should not be mistaken for subcosta-two.

The proximal portion of subcosta is not as a rule fused with radius as most of the drawings of dipterous wings would indicate. The subcosta is always folded under the radial stem, and when wings are examined from above as those mounted on slides, the base of the subcosta is concealed. It would not be strange, therefore, that in specialized wings there should be a fusion of these two closely placed veins. Such a condition has been developed for instance in Scenopinus, Eristalis, Eulonchus, and Calliphora. This fusion extends distal to the region of the humeral cross-vein. The free part of subcosta-two has apparently been merged with this fusion, for in most wings it can not be identified where the fusion exists. Calliphora is an exception. In the wings of this genus the stems of subcosta and radius are fused and the free part of subcosta-two is retained, but is located near the fusion. This condition supports the contention that the free part of subcosta-two is lost through its combination with this fusion. The evidence is conclusive that in all dipterous wings, the single vein in front of radius should always be labelled as subcosta-one, never as Sc, and that the next vein should always be labelled as subcosta-two plus radius-one, regardless of the fact as to whether the proximal free part of subcosta-two is present or not; if wanting it has either fused with the fused stems of radius and subcosta or has atrophied.

ALEX. D. MACGILLIVRAY

UNIVERSITY OF ILLINOIS

## INHERITANCE OF MESOCOTYL LENGTH IN HYBRIDS OF BRACHYTIC MAIZE

EXPERIENCE has shown that deep planting often is desirable with maize if good stands are to be obtained under semi-arid conditions. Most commercial varieties are not adapted for deep planting and the indications are that even in the corn-growing sections the young seedlings frequently are handicapped through planting the seeds below their optimum depth. The depth below which seeds should not be planted is indicated by the length of the mesocotyl, the organ which enables the young seedling to reach the surface.[1]

In considering the utilization of the drought-resistant possibilities of brachytic maize plants the problem of deep planting was encountered, for if full advantage were to be taken of the brachytic characters it was necessary to combine with them the feature of deep planting.

The brachytic variation arose in a hybrid having the Chinese waxy type as one parent.[2] This type of maize, adapted to the low flood plains of the Yangtze, has the shortest mesocotyl as yet found and in consequence requires very shallow planting. It became of interest, therefore, to determine whether this disadvantage, from the standpoint of drought resistance, could be overcome through hybridization with strains not handicapped with short mesocotyls.

Hybrids were made with the Hopi type of maize which Collins had found could be planted 18 cm below the surface, some plants even having mesocotyls 36 cm long. Since the brachytic variation is characterized by shortened internodes, which follow rather definite Mendelian inheritance, and since the mesocotyl is interpreted generally as an internode little success was to be expected in attempting to combine, through hybridization, the antagonistic characters, brachytic internodes and long mesocotyls. In fact, so general is the extension of the brachytic nature of the internodes throughout brachytic plants that it is reflected in the homologous parts of the terminal panicle, as is shown by the reduced length of the branching space.

The first generation seedlings showed mesocotyls longer than the Hopi parent, but the Hopi strain used had been reduced much in vigor through continuous inbreeding.

The plants of the first generation were extremely unpromising, but several self-pollinated ears were obtained. Seeds of these, representing the second generation, were grown in the dark, permitting the complete elongation of the mesocotyl. There was no evidence of Mendelian segregation in this character, as is shown in Fig. 1. To make certain that brachytic segregates were being obtained, since brachytic plants can not be distinguished in the seedling stage, a series of seeds were planted in the field at the bottom of paper mailing tubes set in trenches to permit filling around the plants after the tubes had been removed. The mesocotyls of these plants were measured after their elongation was complete, and the trench filled, the plants being allowed to mature. Of twenty-five mature plants seventeen were of normal stature and eight brachytic. The length of the meso-

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[1] Collins, G. N. A Drought Resistant Adaptation of Hopi Maize, *Jour. Agri. Research.* Vol. 1, No. 4, Jan. 10, 1914.

[2] Kempton, J. H. Heritable Characters of Maize, III Brachytic culms, *Jour. of Heredity,* Vol. XI, No. 3, March, 1920.

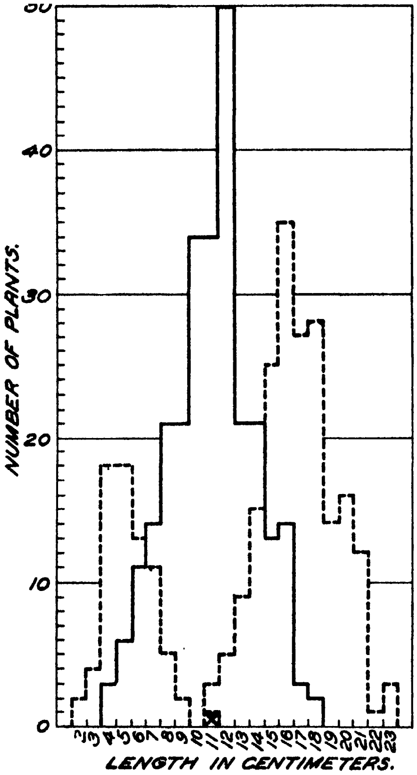

FIG. 1. Comparison of the nature of inheritance of internode length and mesocotyl length. These organs have been considered homologous, one being above, the other below ground. Polygon enclosed in solid line shows distribution of plants with respect to length of mesocotyl in a brachytic-Hopi hybrid ($F_2$). Polygons enclosed in dotted lines show distribution of plants with respect to length of longest internode in a brachytic-Boone hybrid ($F_2$). The small polygon at left represents the brachytic segregates, that at right the normal plants. The square marked X represents a plant classed as brachytic. The polygons are drawn on a basis of 265 individuals; the number of plants in the brachytic-Boone hybrid, while the number of plants in the brachytic-Hopi hybrid was 165.

cotyl varied from 10 to 15 cm in the normal plants with a mean length of 12.1 ± .22, while in the brachytic plants the mesocotyls ranged in length from 10 to 14 cm with a mean length of 11.7 ± .44. It is thus evident that there is no tendency toward a shortening of the mesocotyl, corresponding with the reduction in length of the internodes, of brachytic plants. The very different mode of inheritance of these characters is shown strikingly in Fig. 1, in which the distribution of the plants of the brachytic-Hopi hybrid with respect to mesocotyl length is compared with the distribution for length of internode in a brachytic-Boone hybrid.

It is apparent from this hybrid between brachytic and Hopi that no obstacle of inheritance prevents the combination of long mesocotyl with brachytic internodes, though the particular hybrid studied was unpromising from other standpoints. The failure of the mesocotyl to behave in inheritance in a similar manner to that of the internodes suggests the possibility that this organ is in reality an elongated node as held by Van Tieghem[3] and supported by the fact that roots may arise at any point on its surface.

J. H. KEMPTON

BUREAU OF PLANT INDUSTRY

## CHELYS AND THE PHYLOGENY OF THE TURTLES

IN a recent paper, Hay[1] has brought forth some evidence which at first sight would seem to have considerable bearing on the phylogeny of the Testudinata. Perhaps the most disputed question in the phylogeny of the turtles centers about the relationship of the leathery turtle *Dermochelys*. Some investigators have considered this genus closely allied to the sea turtles, Cheloniidae, while others, such as Hay, would place the leathery turtle in a sub-order by itself, and group all the other recent Testudinata together under another sub-order.

Hay believes that considerable support is given to the latter arrangement by his discovery that the South American Matamata—*Chelys fimbriata*—sometimes possesses a series of irregular bony splinters overlying the carapace and covering parts of the plastron. Hay has examined the shells of six adult specimens of this species and in five of them has found some indication of these splinters. Three of these five shells are in the collections of the American Museum of Natural History and have attracted my attention.

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[3] Van Tieghem, Philippe, Observations anatomiques sur le cotylédon des graminées. *Am. Sci. Nat. Bot.*, S. 5, T. 15, pp. 236–276. 1872.

[1] Hay, O. P., 1922, *Journ. Morph.* 36, pp. 421–441; pls. 1–2.

Hay has postulated that the primordial turtle armature consisted of three layers of bone above the viscera, namely, (1) the ribs, (2) the carapace and (3) a set of bony nodules. Hay compared the series of bony splinters overlying the carapace in five of the specimens of *Chelys* which he examined to the bony nodules or outer bony layer of this primordial but purely hypothetical turtle. According to Hay, most existing turtles possess bony layers 1 and 2; the leathery turtle 1 and 3. *Chelys,* he believed, retained all three layers. A few fossil turtles, according to Hay, possessed some remnants of the outer layer of bone in their so-called epithecals.

It should be noted that all but one of the five specimens of *Chelys fimbriata* found by Hay to possess bony splinters, superimposed on the carapace and lying ventral to the plastron, were old captive specimens. The three specimens belonging to the American Museum, which Hay examined, had all been in captivity for some time. Only two specimens examined by Hay were preserved in the field, and one of these lacked the bony splinters. Captive specimens, especially those retained for any length of time in zoological parks, would be the especial objects of the attacks of parasites. In considering Hay's hypothesis it should also be noted that *Chelys fimbriata* is an excessively specialized Pleurodire and not a form in which one would expect to find ancestral features.

It occurred to me that the critical evidence for Hay's hypothesis should be furnished by the ontogeny of the shell, and the development of these bony splinters. Immature specimens of *Chelys fimbriata* are exceedingly rare in collections. Thanks to the courtesies of the Brooklyn Museum of Arts and Sciences, there is now in the collections of the American Museum an immature specimen captured at Caicarra on the Orinoco River, Venezuela, July, 1907, by Mr. George K. Cherrie. This specimen is apparently an individual of the second or third year. It is 203 mm in total length. The carapace is 124 x 91 mm; the plastron 102 x 72 mm. The greatest width of the head is 51 mm.

Instead of skeletonizing this specimen, I have cleared it by means of a modification of the Schultze method. The entire animal was first stained delicately, with alizarin in order to differentiate any bony splinters, and to define clearly the sutures in the shell. On clearing it was found that the shell had not reached its full development. Three foramina were present along the median axis of the plastron. The largest of these foramina measured 13 x 10 mm. The carapace and plastron were not ankylosed together, a small space being present between them. The carapace exhibited a series of nine foramina along each side between marginals and costals. The bones of the shell were massive. The shell, although incomplete, was by no means embryonic. Practically all of the regions, which in the adult shell exhibited a series of bony splinters, were already well formed.

A careful examination of these regions under a strong transmitted light has failed to reveal any indication of the splinters. It is obvious that this specimen, like one of the adults examined by Dr. Hay, does not possess them. One may argue, of course, that in my specimen, although 203 mm in length, the splinters have not yet developed. Still, one would expect that, if these splinters have such a great phylogenetic significance, they would at least be represented by cartilaginous or fibrous anlagen. It is, perhaps, unwise to draw any general conclusion from a single observation. Nevertheless, as Dr. Hay's hypothesis is based upon such a limited series of specimens, it seems to me that the evidence offered by my specimen is significant. Hay's hypothesis should not be accepted without additional material.

In conclusion, it may be said that the ontogeny of the shell of *Chelys fimbriata* lends no support to the view that the splinters of bone, sometimes found on the shell of the adult, are remnants of a former layer of bone, homologous to the definitive shell of the leathery turtle. These splinters seem to be bony deposits formed over injuries received either during captivity or rarely in nature.

G. K. NOBLE

THE AMERICAN MUSEUM OF NATURAL HISTORY,
NEW YORK CITY

## A NOTE ON THE THEORY OF SEX DETERMINATION

THE recent important work of Bridges (1921, 1922) on triploid Drosophila has shown that sex is determined in this form by the relation between the X chromosomes and the sets of autosomes present in an individual. Bridges has concluded from his data that the effective relation is the *ratio* between number of X chromosomes and the number of autosomes. This ratio is the same in completely diploid ($2X + 2A$, where $A =$ one complete set of autosomes) and completely triploid ($3X + 3A$) individuals, and these individuals are females in Drosophila.

That the autosomes as well as the X chromosomes are concerned in the determination of sex has hitherto met with no such definite demonstration as that given by Bridges. In fact, the older chromosomal hypothesis ignored the autosomes and regarded maleness and femaleness as depending on the presence of one or two X chromosomes respectively (or vice versa in some cases). More recently, Goldschmidt has subscribed to the view that sex rests on the resultant of two opposing factors, but although he believes one of these to be located in the X chromosome, he regards the other as situated in the Y chromosome or else the cytoplasm of the egg.

In considering Bridges' hypothesis, it becomes evident at once that a haploid ($X + A$) Drosophila (which has not yet been discovered) must be a female. This introduces a difficulty which has sooner or later always been encountered in older hypotheses. It lies in our conception of chromosomal conditions in animals where males are haploid. In several groups (Rotifera, Thysanoptera, Aleyrodidae, Hymenoptera and Acaridae) there are forms in which it appears almost certain that females are diploid and males haploid. Regardless of how such a condition was brought about, it is commonly assumed that these types represent nothing but a modification of the ordinary type of sex determination. If Bridges' conclusions be accepted that view is no longer tenable, and we are forced to conclude that the sex-determining mechanism is of a different type altogether in the two cases. The purpose of the present note is to show that such a conclusion is not necessary, because the ratio view is not proven.

Bridges' results show clearly that the autosomes have, as a whole, a male-producing tendency and the X chromosomes a female-producing tendency. Let us arbitrarily call maleness the plus and femaleness the minus direction; let us assign a numerical value of $-6$ to the X chromosome, and one of $+2$ to one set of autosomes (or A). It is then to be assumed that the effective relation is the *algebraic sum* of X and A, rather than their ratio, a procedure which will be familiar to those who have read

Goldschmidt's papers on sex determination in the gypsy moth.

The remarkable series of forms identified in Drosophila by Bridges, with the addition of the haploid form, will then work out as follows:

| Name | Constitution | Algebraic Sum |
|---|---|---|
| super-male | X + 3A | 0 |
| male | X + 2A | —2 |
| haploid | X + A | —4 |
| intersex | 2X + 3A | —6 |
| diploid female | 2X + 2A | —8 |
| triploid female | 3X + 3A | —12 |
| super-female | 3X + 2A | —14 |

If we suppose the threshold value for maleness to be at —5 and that for femaleness to be at —7, the result is consistent with the view that the haploid Drosophila may be male. The bee may thus have essentially the same type of sex determination as Drosophila. It is not important in this connection whether we suppose that the drone has a single X chromosome, or whether the material represented by the X chromosome in Drosophila is distributed over the autosomes in male Hymenoptera.

No special significance is to be attached to the numerical values assigned to X and A; and it seems highly improbable that their effect depends on so simple a mathematical function as that employed here. The important point is that the data at present available do not demonstrate that the ratio between the number of X's and the number of autosomes is the effective element in the situation.

FRANZ SCHRADER
A. H. STURTEVANT

BRYN MAWR COLLEGE AND
COLUMBIA UNIVERSITY

## THE PARALLEL CHARACTERS "CROSSVEINLESS" AND "VERMILION" IN DROSOPHILA WILLISTONI

IT has been shown by Lancefield and Metz[1] that certain sex-linked characters in Drosophila willistoni resemble characters in Drosophila melanogaster, Drosophila virilis and Drosophila obscura, not only in appearance but in their linkage relations. Attention may be called particularly to the characters "scute" and "yellow," which are almost completely linked and which resemble the similarly linked characters of like names in the other species, with the exception of virilis. In virilis scute has not yet been found, but yellow is present. The relations of these and other "parallel"[2] characters in the respective species has suggested that homology may be involved. Such a view is strengthened by the additional "parallels" crossveinless and vermilion considered below.

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[1] R. C. Lancefield and C. W. Metz, AMER. NAT., lvi: 211, 1922.

Crossveinless in D. willistoni is characterized by the absence of both cross veins in the wings and by a slight swelling of the fifth and, to a lesser extent, of other veins at their apices. With the exception of the slight swelling of the veins this character appears to be a duplicate of the crossveinless in D. melanogaster[3] and in D. virilis.[4] In D. obscura crossveinless has not yet been found.

Vermilion in D. willistoni has vermilion colored eyes. It also has whitish instead of yellowish ocelli. In both of these respects it resembles the sex-linked vermilion in D. melanogaster,[5] D. virilis[6] and D. obscura.[7]

The sex-chromosome "maps" representing the linkage relations of sex-linked characters in these species are given in the accompanying figure. Symbols are included only for the characters under discussion; others are indicated merely by cross lines marking the loci. These maps are arranged so that the locus of yellow, which is common to all, comes on a common line. This is used as the zero point in designating map distances.

In D. willistoni the amount of crossing over between scute and yellow is negligible; only one certain case has been found. This one, however, was such as to indicate that the locus of scute is above that of yellow. Yellow and crossveinless have given a crossover value of 2.1 per cent. on the basis of 1,435 flies, and crossveinless and vermilion have given a value of 0.3 per cent. on the basis of 1,351 flies. Tests involving the genes for scute, yellow and crossveinless in one chromosome and vermilion in the other gave the following crossover classes among 891 flies: crossveinless 8, scute yellow vermilion 6, "wild type" 3. The latter appeared singly in three different bottles, making it practically certain that they represent crossovers and are not due to contamination. The results indicate that the order of the genes is scute yellow crossveinless vermilion, which agrees with the order in the other species so far as known.

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[2] The term "parallel" is used to designate mutant characters similar in appearance and (usually) in linkage relations, in different species where homology can not be proved by crossing.

[3] Bridges, C. B., *Proc. Nat. Acad. Sci.*, 6: 660, 1920.

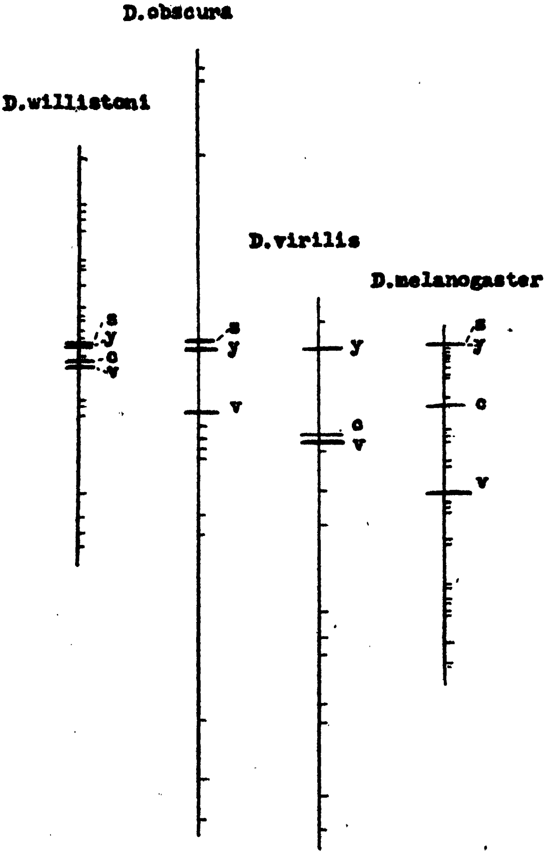
[4] Weinstein, A., *ibid.*, 6: 625, 1920.

[5] Morgan and Bridges, *Carneg. Inst. Wash.*, Pub. 237, p. 27, 1916.

[6] Metz, Moses and Mason, *ibid.*, Pub. 328.

[7] D. E. Lancefield, *Genetics*, 7: 335, 1922.

When the accompanying maps are compared they reveal three features which require consideration here. In the first place the series of loci under consideration falls near the end of the maps in two cases (melanogaster and virilis), but near the middle in the other two. This is believed to bear a significant relation to the fact that in the two former species the X-chromosomes are short and rod-like, while in the latter they are about twice as



long and are V-shaped.[8] Such a correlation between chromosome proportions and map proportions led to the suggestion[9] that the rod-like X's of melanogaster and virilis may possibly correspond to one arm of the V-shaped X-chromosome in willistoni and obscura. The evidence as a whole is still in accord with this view.

A second feature revealed by the maps is that although the serial order of the loci considered here is the same in all four cases,[10] the map distances involved differ considerably. In willistoni the distance from scute to vermilion is approximately 2.5 units, in obscura it is about 15 units, in virilis about 25 units and in melanogaster about 33 units. In all but the last case, however, these differences are associated with differences in total map lengths which indicate general differences in frequency of crossing over in the X-chromosomes. For instance, crossing over in the X-chromosome of obscura appears to be more than twice as frequent as in the willistoni X. Likewise crossing over appears to occur more frequently in the virilis X than in the melanogaster X. When the *relative* positions on the maps are considered the agreement is closer.

But there is one conspicuous exception, and this brings out the third feature requiring consideration. In willistoni and virilis crossveinless and vermilion are very closely linked. In melanogaster, on the other hand, the locus of vermilion falls at a point on the map nearly 20 units below that of crossveinless, and between the two are several other identified loci. It seems necessary to conclude in this case either that one of the two characters is not homologous to those in the other species, or else that a rearrangement of genes is involved. The evidence (which will be given in detail elsewhere) at present favors the latter view.

Only a portion of the known sex-linked "parallels" are included above; others, particularly singed and forked, might be added to the series, but a complete discussion is not intended in this brief note.

CHARLES W. METZ
RUTH M. FERRY

DEPARTMENT OF GENETICS,
CARNEGIE INSTITUTION OF WASHINGTON

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[8] Metz, C. W., AMER. NAT., 1:587, 1916.

[9] See notes 1 and 6 for references.

[10] Scute and yellow in melanogaster appear to be completely linked; hence their relative positions are not known.

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# THE ORIGIN AND DISTRIBUTION OF THE ANURA

PROFESSOR MAYNARD M. METCALF
THE ORCHARD LABORATORY, OBERLIN, OHIO

THIS paper is a discussion of the former existence of land bridges from east to west between continents of the southern hemisphere of the Earth. There are to-day two north and south intercontinental bridges, the Isthmus of Panama connecting North America and South America, and the Isthmus of Suez connecting Asia and Africa.

Practically all geologists, paleontologists and biogeographers agree that during the later Tertiary period there was eastern and western union of North America with other continents:—(1) with Europe by way of Greenland, Iceland, the Faroe Islands and the British Isles; (2) with Siberia by way of Alaska.

Most paleogeographers—including geologists (emphasizing evidence from Earth structure), paleontologists (emphasizing evidence from fossils) and biogeographers (emphasizing evidence from the genetic relationships and geographic distribution of animals and plants) agree that during the Cretaceous period there was an ocean channel running westerly and north from the Gulf of Mexico to the Arctic Ocean, cutting off the westernmost portion of North America from the rest of the continent, and that the narrow western land strip so formed was connected at its northern end with Siberia and at its southern end with the mountainous region in central

Central America (fig. 2). Scharff and some others believe there is sufficient biogeographic evidence to indicate that the southern end of this east-Pacific land strip was prolonged to include Ecuador and the Galapagos Islands; and Scharff, on the basis of a large amount of evidence from present day animals and plants, carries this land strip as far south as Chile and Patagonia.

Most paleogeographers now recognize a late Tertiary connection between Central America and the West Indies. Vaughan (1919), for example, judging chiefly from the present contour of the floor of the Caribbean Sea and from the geology of southern Central America, places one bridge between Yucatan and Cuba and a second bridge between Honduras and Jamaica.

As to the southern hemisphere opinion is more divided, but there is a large amount of evidence, accepted by numerous geologists, paleontologists and biogeographers, to indicate:—(1) a connection, or connections, between South America and Australasia (usually regarded as late Cretaceous or early Tertiary); (2) between Africa and South America—some opinion accepting (*A*) a bridge from northern Africa to the Guianas and (*B*) a bridge from South Africa to Patagonia, both these bridges being usually regarded as Mesozoic, though by some they would be extended into the earliest Tertiary.

Almost all paleogeographers, if not all, believe that Australasia was united to the Malaysian islands and the Asian continent during part of the Mesozoic (Jurassic).

This article is an examination of certain discussions of the idea of east and west bridges between southern continents, in which such southern intercontinental connections have been denied.

Dr. W. D. Matthew, in 1915, published certain theses as to animal dispersal which may to advantage be studied critically by the host-parasite method (Metcalf 1921, 1922, 1923). These theses were reiterated by Dr. E. R. Dunn, last December, at the Boston meeting of the scientific societies and were specifically applied to the Amphibia. Let us reexamine these propositions in the light of the dispersal of the Anura and their Opalinid parasites.

Matthew's familiar theses are:—

(1) "Secular climatic change has been an important factor in the evolution of land vertebrates and the principal known cause of their present distribution.

(2) "The principal lines of migration in later geologic epochs have been radial from Holarctic centers of dispersal.

(3) "The geographic changes required to explain the present distribution of land vertebrates are not extensive and for the most part do not affect the permanence of the oceans as defined by the continental shelf.

(4) "The theories of alternation of moist and uniform with arid and zonal climates, as elaborated by Chamberlin, are in exact accord with the course of evolution of land vertebrates, when interpreted with due allowance for the probable gaps in the record.

(5) "The numerous hypothetical land bridges in temperate, tropical and southern regions, connecting continents now separated by deep oceans, which have been advocated by various authors, are improbable and unnecessary to explain geographic distribution. On the contrary the known facts point distinctly to a general permanency of continental outlines during the later epochs of geologic time, provided that due allowance be made for the known or probable gaps in our knowledge.

(6) [p. 180] "Whatever agencies may be assigned as to the cause of the evolution of a race, it should be at first most progressive at the point of original dispersal, and it will continue this progress at that point in response to whatever stimulus originally caused it and spread out in successive waves of migration, each wave higher than the previous one. At any one time, therefore, the most advanced stages should be nearest the center of dispersal, the most conservative stages farthest from it. . . . In fact, it is the environment itself, biotic as well as

physical, that migrates, and the primitive species are those which have followed it, while those that remained have had to adapt themselves to a new environment and become altered thereby.

(7) [p. 311] "The distribution of the Reptilia [intended, apparently, to include Amphibia] appears to be in conformity with the principles here outlined, and extends their application to the Mesozoic era. The distribution of birds and fishes and of invertebrates and plants is probably in accord with the same general principles, modified by differences in methods of dispersal."

Matthew's figure of the distribution of three families of Anura is here given (Fig. 1), corrected for nomenclature and for an inadvertent exchange of family names.

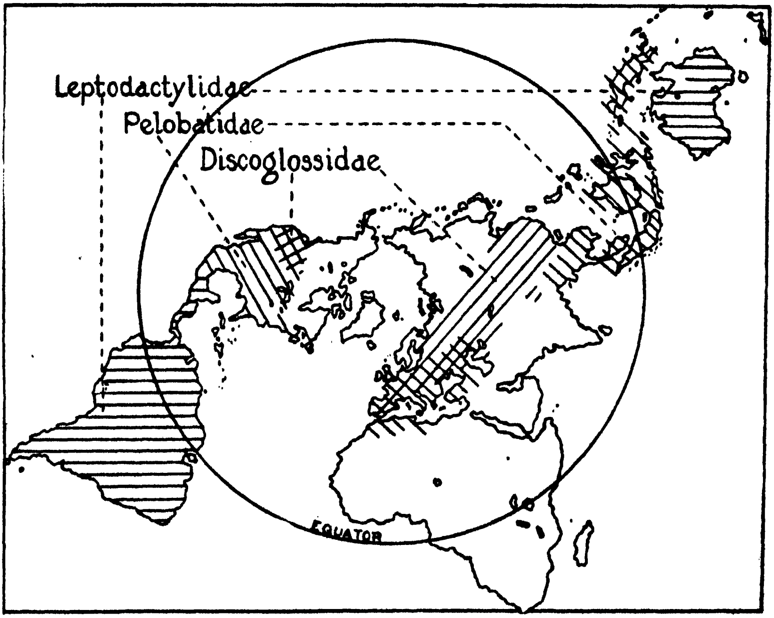

FIG. 1. DISTRIBUTION OF THREE FAMILIES OF ANURA, AFTER MATTHEW (MODIFIED FOR NOMENCLATURE AND FOR AN INADVERTENT EXCHANGE OF FAMILY NAMES).

To these theses of Matthew, Dunn (1923) adds [p 135] "The center of dispersal is best determined by the geographic center of the group range."

Matthew's principles of dispersal are attractive, especially his summary of climatic changes and their effects upon faunas and floras.[1] The almost geometric treatment of migration waves (Matthew 6 and Dunn) suggests hesitation and questioning because of the mathematical perfection of the hypothesis. So far as concerns mid-Tertiary and later Mammalia it may well be that Matthew has correctly sketched the broader aspects of their dispersal. Early Tertiary conditions seem doubtful, and the application of his theses to Mesozoic forms seems still more doubtful. We will here review merely part of the evidence from the dispersal of the tailless Amphibia and their Opalinid parasites.

Of the Hylidae Matthew writes: "The Hylidae are today chiefly South American and Australian, but a few members *still*[2] inhabit North America. They are not found in Africa [error] or in the oriental region [error] where it seems reasonable to suppose that they have been displaced by the true frogs (Ranidae),[3] peculiarly varied and abundant in these regions." Dunn, having assigned to *Bufo* "dispersal from a northern center," writes: "Similarly *Hyla* is the only genus of Hylidae common to South America and to any of the other continents and it, as does *Bufo*, has a wide northern range." He believes in a northern origin for this family.

The evidence seems to me to point to tropical South American origin of the Hylidae and their spread in two lines of migration: first, westward across the Pacific Ocean to Australia, Papua and the Solomon Islands, not New Zealand,[4] (Fig. 2); and, second, northward to Central America and North America and on by way of an Alaska-Siberia route to Euro-Asia and northern Africa.

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[1] Borrowed largely, as he says, from Chamberlin.

[2] Italics mine.

[3] Frogs of the family Ranidae hardly compete with the tree frogs (Hylidae). Their habitats and habits are too different.

[4] As long ago as 1898 Papua was known to have 7 species of *Hyla*, and the Solomon Islands 3. The presence of a Gastrophrynid ["Engystomatid"] (*Calophrynus*) in Samoa and of Limnodynastes, a Leptodactylid, in the New Hebrides is of interest in connection with the hypothesis of a trans-Pacific bridge from South America to Australasia.

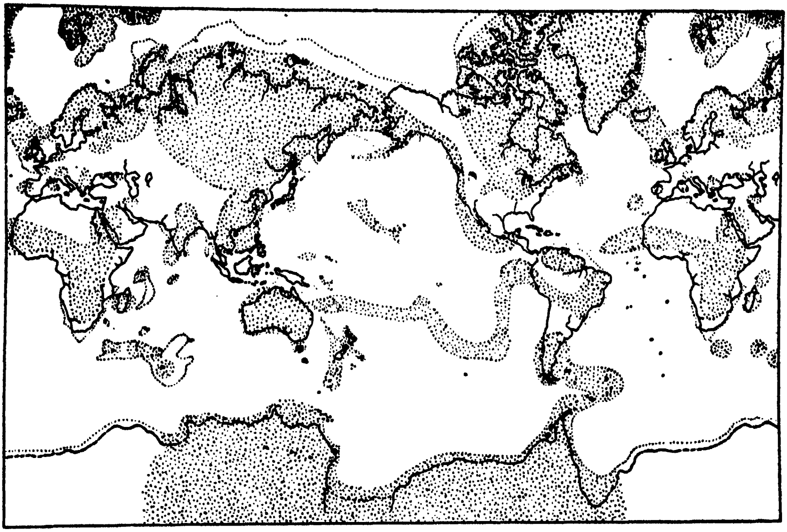

FIG. 2. RELATIONS OF LAND AND SEA AT THE CLOSE OF THE MESOZOIC OR BEGINNING OF THE TERTIARY ERA.

The trans-Pacific bridge follows the general line of the southern shallows and includes Samoa (home of *Calophrynus*, a Gastrophrynid) and the New Hebrides (*Limnodynastes peronii*, an Australian Leptodactylid). The Solomon Islands (Hylas 3, Ranas 3, *Cornufer* 2, *Batrachylodes*, *Ceratobatrachus*, all endemic) and Papua (*Rana* 3, *Cornufer* 3, *Stenophryne*, *Callulops*, *Xenobatrachus*, *Xenorhina*, *Genophryne*, *Crinia*, *Hyla* 7, *Ranaster*, *Asterophrys*) indicate an early connection with Australia and a later connection with the Malay Islands. They are not united to Australia in this map, for their union may well have been somewhat later. In a little later period Australia and New Zealand would be shown united to Antarctica.

Note the land strip from Siberia to Alaska and the western American coast as far south as the mountains of central Central America. At a little earlier period this would be shown connected to the south with Ecuador and the Galapagos Islands. Hawaii (if, as is improbable, *Bufo dialopus* be a native species), probably, then, had at about this time an Arctogean connection by which its *Bufo* entered. That this was to the west, if it existed, is probable in view of the fact that the western islands of the group are the older, the group having been advancing to the eastward by the rising of new land at the eastern end of the group and the subsidence of land to the west, the movement of the group as a whole being like that of a wave. This eastward movement is said now to have ceased.

The connection of Patagonia to Antarctica may have disappeared before the Antarctic union with Australia and New Zealand was established, making here a similar land wave moving from east to west. There is some evidence, not conclusive, that the migration of animals at about this time was westward rather than eastward between America and Australia.

The earlier (Jurassic and early Cretaceous) connection between Patagonia and southern Africa is not shown, and the union of northern Africa and the Guianas is disappearing. There is perhaps some indication, emphasized by some zoögeographers, that the Africa-South America connection or connections may have persisted into the early Tertiary.

[Map compiled, with modifications, from Arldt, Schuchert, von Ihering, Scharff and Haug.]

The several genera of the Hylidae are very similar to one another; *Chorophilus, Acris* and *Agalychnis* might well be regarded as subgenera of the genus *Hyla.*

The Hylidae and the Leptodactylidae ("Cystignathidae") are very near relatives and in all likelihood arose from common ancestors. The Leptodactylidae now occur in tropical America, New Zealand (*Liopelma,*[5] 2 species), Tasmania, Australia, Papua, the New Hebrides (the Australian species *Limnodynastes peronii*). The Hylidae (Fig. 3) are abundant in tropical America and Australia, are well represented in Tasmania, Papua (7 +) and the Solomon Islands (3), but not in New Zealand, are present (1 species, *Hyla arborea chinensis*) in Formosa (Vogt, 1911), are abundant in North America and a few forms (probably best regarded as offshoots from a single immigrant species, perhaps as one species with half a dozen or so subspecies) are found in Euro-Asia (including eastern and southeastern Asia, Formosa, India, the

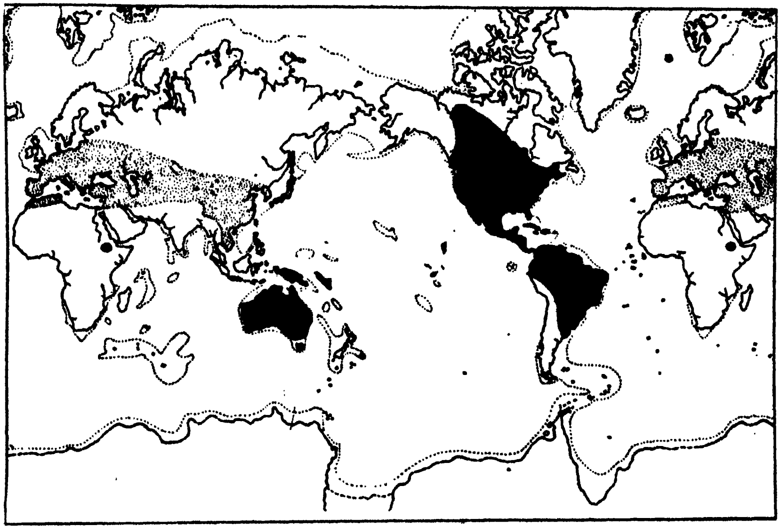

FIG. 3. DISTRIBUTION OF HYLIDAE.

The stippled areas are occupied only by *Hyla arborea* and about half a dozen closely related forms, perhaps best treated as subspecies. The status of "*Hyla wachei*" from Abyssinia is still uncertain.

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[5] First described as a Discoglossid.

Caucasus, Asia Minor, Europe), in northernmost Africa and in Abyssinia.[6] Fossil Hylids or Leptodactylids have not been reported, so far as the author knows.

The presence of even a few Hylids in Euro-Asia seems to give comfort to the advocate of a northern origin of this family, rendering it, at first thought, more likely that the Australasian Hylids may have entered their present habitat from the north by way of Malaysia. There are, however, definite difficulties in the way of such a hypothesis.

(1) The Euro-Asian Hylids are much more nearly related to North American species than they are to Australasian species.

(2) The Opalinid parasites of the Euro-Asian Hylids,[7] so far as known, are of a modern subgenus (*Opalinae angustae,* evolved, apparently, in the Pliocene), are of North American origin (Fig. 4), and are utterly different from any Opalinids known in Australasia. *Opalina obtrigona* was the Opalinid found in all the infected Hylas from Euro-Asia. This is perhaps the most modern of all Opalinidae. The Australian Hylids, on the other hand, have been found to carry Opalinids only of the most archaic genus, *Protoopalina,* a genus of world-wide distribution. The Euro-Asian Hylid parasite, *Opalina obtrigona,* is almost identical with the North American species *O. obtrigonoidea,* which occurs in several North American genera, including Hylids of five species.

A few words as to the classification and occurrence of the Opalinidae will emphasize the evidence they give as to the origin and dispersal of their hosts. In the family Opalinidae are two subfamilies and four genera, as follows:

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[6] The reference of this Abyssinian form to the family Hylidae has been questioned.

[7] But three Palearctic Hylas have been successfully searched for Opalinids —*Hyla arborea* from western Europe, *H. arborea savignyi* from Jerusalem and *H. arborea japonica* from Japan. One individual each of three other subspecies (*chinensis, meridionalis* and *stepheni*) have been opened but found uninfected.

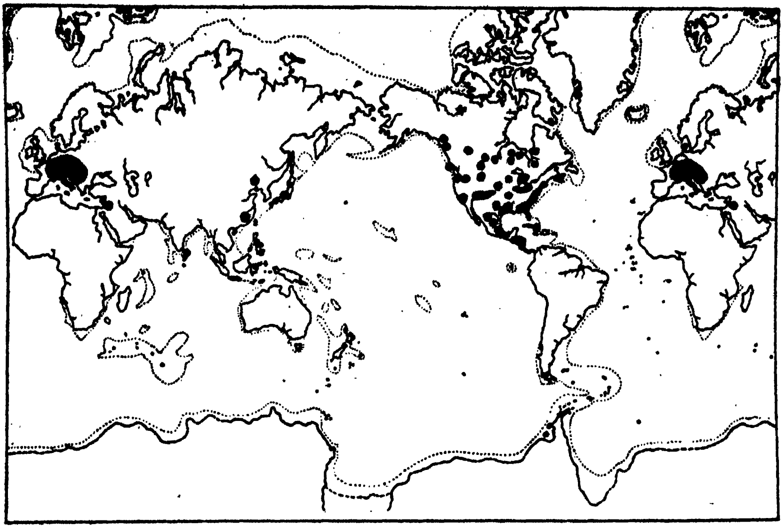

FIG. 4. DISTRIBUTION OF THE OPALINAE ANGUSTAE.
The genetic relationship of the Ceylonese *Opalina virgula* to this subgenus is doubtful, because of both its structure and its geographical position. All other Palearctic records shown are of *Opalina obtrigona* only.

Opalinidae
  *Protoopalininae* (2 nuclei)
    *Protoopalina* (cylindrical, or at least not much flattened), 9 subgenera
    *Zelleriella* (much flattened)
  *Opalininae* (multinucleated)
    *Opalinae latae* (broad forms of oriental origin)
    *Opalinae angustae* (narrow forms of Nearctic origin).

The indications are strong that *Zelleriella* arose in tropical America from *Protoopalina*; that *Cepedea* evolved from *Protoopalina,* probably in southern Asia; that *Opalina* (broad form) was derived from *Cepedea,* apparently in Euro-Asia; that the *Opalinae angustae* arose in southwestern North America or in Central America when Hylids, coming north from South America, first met Bufos and Ranas bearing broad *Opalinae,* adopted these parasites and changed them to the narrow form. The change of form of the *Opalinae* in Hylid hosts, occurred probably after the middle Pliocene, when the Isthmus of Panama was definitely formed (Vaughan, 1919), though it is possible that Hylids entered Central America and western North America earlier in the Tertiary by way of a land strip somewhat to the westward of the present Isthmus of Panama (Fig. 2). The presence of broad *Opalinae* in America before the later Tertiary is, however, improbable, the genus *Opalina* being apparently of late Tertiary origin in Asia.[8] Narrow *Opalinae* are found only in North America and Central America, except for the one species, *O. obtrigona,* in the Euro-Asian *Hyla arborea* and its subspecies. It seems pretty clear that *Hyla arborea,* or its immediate ancestor, very closely related to western North American species, passed from North America by the Alaska-Siberia route, across Euro-Asia and into northern Africa, carrying with it the North American narrow *Opalina* which now discloses the place of origin of its host. It seems equally clear that the Australasian Hylas did not come from Euro-Asia, for there are no Euro-Asian Hylas known to-day except those of close North American affinities and we know no Palearctic fossil Hylas. It seems wholly unlikely that Hylids, whether of Nearctic or of Palearctic origin, could have entered Australasia from the north without leaving in Euro-Asia and Malaysia species showing affinity to present Australasian tree frogs.

No multinucleated Opalinids are known from Australasia. If the Australian Hylas had entered from Asia they should have brought multinucleated Cepedeas or Opalinas, such as are found in Nearctic Hylids, unless they left Asia before the evolution and presence there of these multinucleated genera. All the indications seem distinctly against the hypothesis of the Australasian Hylids having entered Australasia from the north.

The Leptodactylidae present equally difficult phenomena to the one who seeks to explain their present distribution upon the theory of northern origin (Fig. 5). They

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[8] For fuller discussion of these relations see Metcalf (1923).

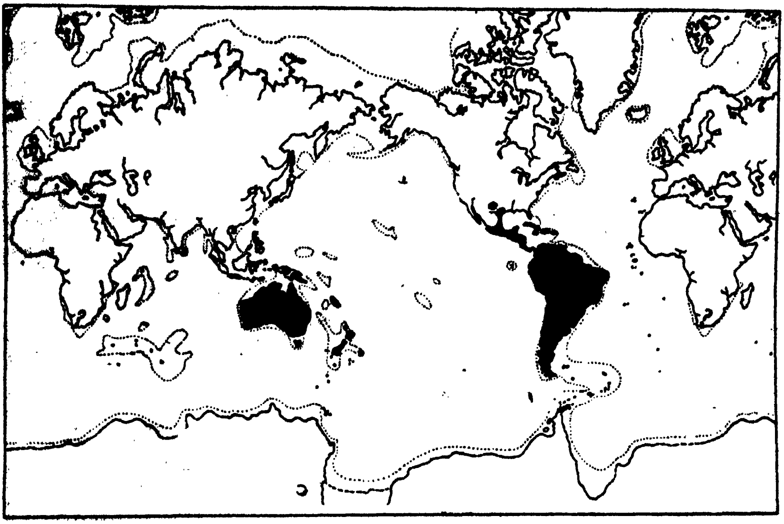

FIG. 5. DISTRIBUTION OF LEPTODACTYLIDAE.
The question mark in southern Africa indicates doubt that has been expressed as to the genetic relationship of its genus *Heleophryne* to the Leptodactylids.

are to-day confined to tropical America (ca. 250 species), New Zealand (*Liopelma,* 2 species), Tasmania (4 species), Australia (ca. 30 species), Papua (*Genophryne* and *Crinia* and perhaps others of recent record) and the New Hebrides Islands (*Limnodynastes peronii,* also in Australia), with the possible addition of southern Africa, from which region *Heleophryne* (2 species) has been reported. The American and Australian Leptodactylids bear parasitic Zelleriellas so similar that they may be specifically identical, and the genus *Zelleriella* (Fig. 6) is known only from tropical America and its North American fringes and from Australia.[9] If the Leptodactylids

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[9] Bezzenberger's (1904) report of a *Zelleriella* (*macronucleata*) from "Asia" is so vague as to locality, and the likelihood of confusion as to locality is so considerable, that this species can not be taken into account. The species may be identical with an Australian or tropical American species or both. See Metcalf (1923). Recent as yet uncompleted studies of certain Cepedeas, made by a friend, and to which it is not appropriate now to refer more fully, cast grave doubt upon *Zelleriella macronucleata* being an adult form or even a *Zelleriella* at all. The occurrence of this Opalinid in "Asia" gives no evidence upon the question here under discussion.

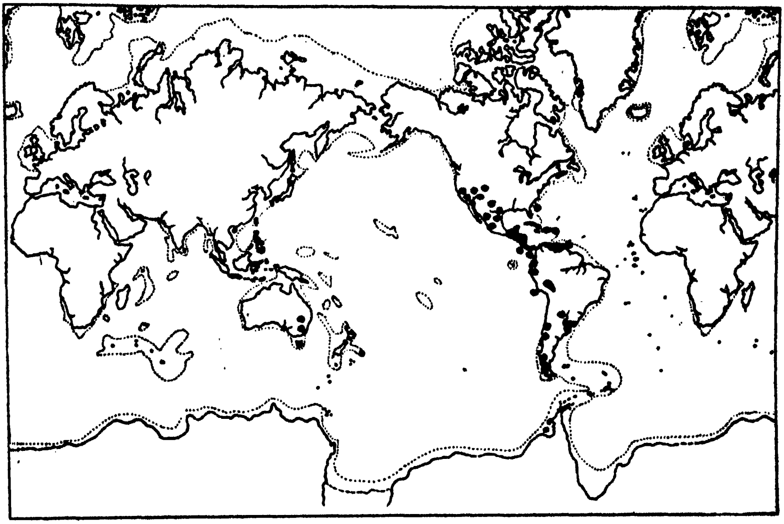

FIG. 6. DISTRIBUTION OF ZELLERIELLA.

arose in the north and spread southward to South America and Australasia, how is it that no Leptodactylids or Zelleriellas are found in Euro-Asia or in north-temperate North America?[10] In tropical America and in temperate South America and Australia the Leptodactylids are vigorous dominant forms. If Leptodactylids, indeed, were once in Asia and have become extinct there or been driven out, their *Zelleriella* parasites should now be found in the Asian Bufos, for toads readily adopt any Opalinids with which they come into contact. Leptodactylids endure well the cold of Patagonia and of the high Andes, so they can not well have been driven out of Euro-Asia by inclement climate. There seem no indications that they ever were in Palearctica, and they have now reached only the southern fringes of the Nearctic region. Unless further search reveals Leptodactylids or Zelleriellas or both in Asia, there seems scant possibility of the former presence of Leptodactylids in Asia. *Zelleriella* seems a comparatively modern genus, probably of early or middle Tertiary origin, and its spread from South America to Central America and North America was probably in Pliocene times, though it may possibly have reached these northern lands earlier, by a land route lying to the west of the Isthmus of Panama (Fig. 2), at a time before the present Isthmus was formed.

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[10] No fossil Leptodactylids are known from Arctogea.

We should note also that probably the most archaic subgenus of the genus *Protoopalina* (Fig. 7) is represented in Australian and Patagonian Leptodactylids and that Johnston (1912, 1914) reports the Anuran Trematoda of Australia as showing far closer affinities with those of South America than with those of any other region.

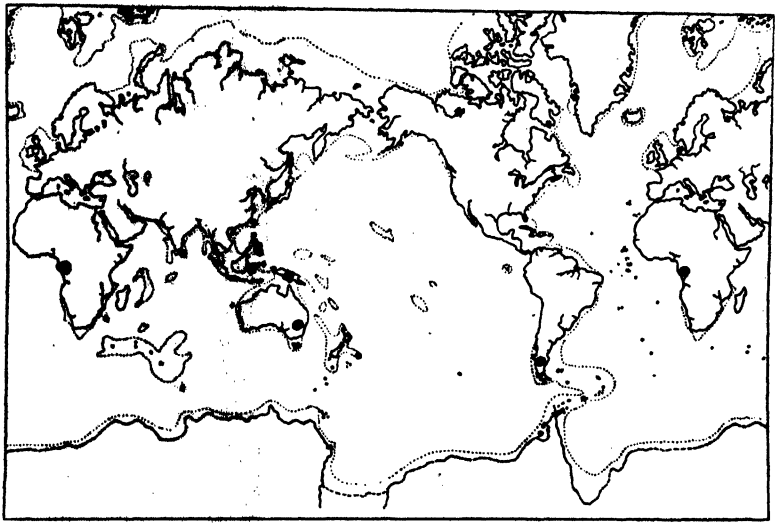

FIG. 7. DISTRIBUTION OF THE MOST ARCHAIC SUBGENUS OF PROTOOPALINA.

The evidence seems clear that the Leptodactylids arose in South America and that *Zelleriella* evolved in these South American hosts. Also the evidence seems strong that neither Leptodactylids nor Zelleriellas have ever lived in Asia. How then did Australasia (including New Zealand and Papuasia) get its Leptodactylids and their parasites the Zelleriellas? The answer seems of necessity to be—by some southern route. And the distribution of the Hylidae also calls for a southern route between tropical America and Australasia, there being no palearctic Hylids except such as by their genetic relationships and their parasites are shown to have emigrated very recently from North America.

The New Zealand Liopelmas were described as Discoglossids, but further study has now led to their classification among the Leptodactylids.

What shall we say of *Heleophryne* in South Africa? This form has an arciferous sternum and has been classed as a Leptodactylid. The suggestion has, however, been made that it may be genetically a Ranid which has not completed its development from the arciferous to the firmisternous condition. If it be genetically a Leptodactylid, it would seem to indicate the origin of the Leptodactylidae at or before a period when southern South America and southern Africa were connected by a trans-Atlantic bridge—often called Archiplata. This southern trans-Atlantic bridge is usually regarded as having become permanently interrupted in the Cretaceous period, though by some it has been thought to have persisted into the Tertiary. If the African *Heleophryne* proves to be a Leptodactylid, it would tend to date the origin of this family somewhat earlier geologically than the South America-Australia evidence would necessitate. If *Heleophryne* should be found to bear *Zelleriella* this would seem evidence, difficult to combat, that South Africa and South America were once united by a southern migration route.

The Hylidae and the Leptodactylidae are among the more modern families of Anura, possibly more modern than any others of the usually recognized families, though the Ranidae are in some respects structurally more developed. If these comparatively modern forms do not fit into Matthew's schema of dispersal, it is likely some of the other families may not do so.

The present distribution of the genus *Rana* (Fig. 8) and a study of its Opalinid parasites indicates a probable northern origin of this genus. Except for a single species in northern South America, several species in Papua, one

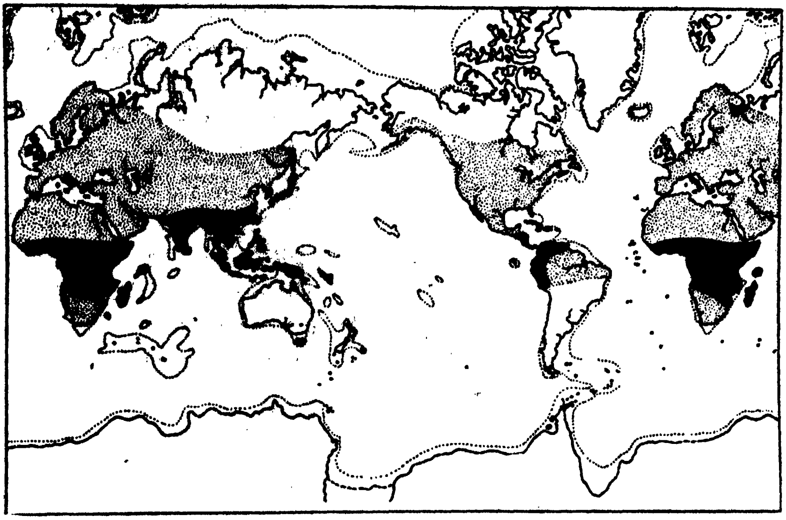

FIG. 8. DISTRIBUTION OF RANINAE.

The presence of genera other than *Rana* is indicated in black. *Rana* is found over both the stippled and the black areas except that it is absent from Madagascar and the Seychelles Islands.

Papuan species in the northernmost tip of Australia, and three species in the Solomon Islands, they have not penetrated into the southern hemisphere except in Malaysia and in Africa. Their entrance into the Malaysian Islands and Papuasia was probably in the late Tertiary, and their entrance into tropical Africa may well have been by way of the Nile valley, this also in later Tertiary times. Fossil Ranas are known from European rocks of the lower Miocene and perhaps of the upper Oligocene. Other genera of the same subfamily, *Raninae,* have an Equatorial distribution and we seem to find nothing in themselves, their fossil remains,[11] or their Opalinids, to determine definitely whether their original habitat was in "Equatorian" lands or was northern. The former has seemed to me the more probable (Metcalf, 1923).

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[11] The reported presence of *Oxyglossus* in the Eocene of Wyoming is difficult to accept, at least without a very thorough review of both the biotic and geologic evidence. This seems, indeed, to be the same form which Moodie (1914) describes from Marsh's specimens as *Eobatrachus agilis* Marsh. Moodie regards it as probably a Bufonid, and he assigns it to the Jurassic. It may be lower Cretaceous.

The *Dendrobatinae* (Fig. 9), another subfamily of the Ranidae, are of exclusively southern habitat to-day and I know of nothing in themselves or in their Opalinid parasites to suggest migration at any time southward from a former Arctogean home.

The Ranid *Ceratobatrachus,* the sole representative of the *Ceratobatrachinae,* is known only from the Solomon Islands and apparently throws little light upon the hypotheses under discussion. The Solomon Islands have strong Papuan affinities in their Anuran fauna. There is zoogeographic evidence of Papua having had Malaysian connections since it separated from Australia. The development of a subfamily of Ranids (*Ceratobatrachinae*) exclusively in the Solomon Islands, and the fact that all the Anura in the islands (9 species of 3 families) are endemic, makes probable an early separation of these islands from Papua, though subsequent to the separation of Papua from Australia.

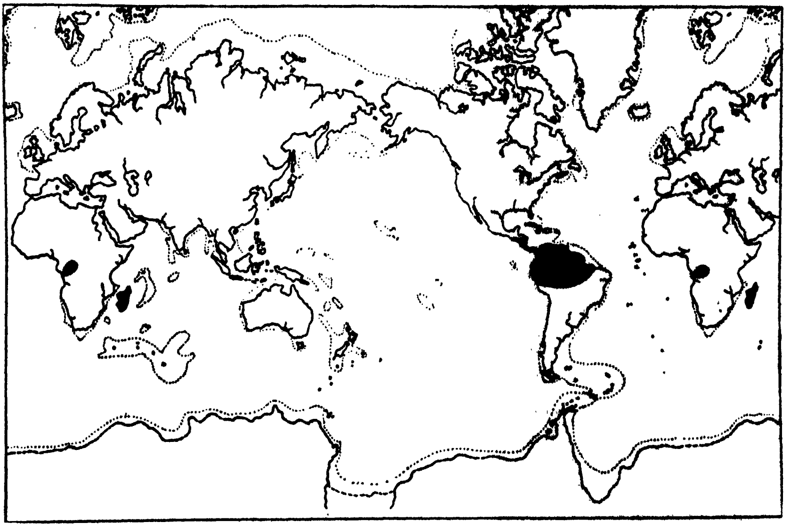

FIG. 9. DISTRIBUTION OF DENDROBATINAE.

The Gastrophrynidae ["Engystomatidae"] (Fig. 10), another firmisternous family and probably comparatively modern, are to-day confined to the tropics and to

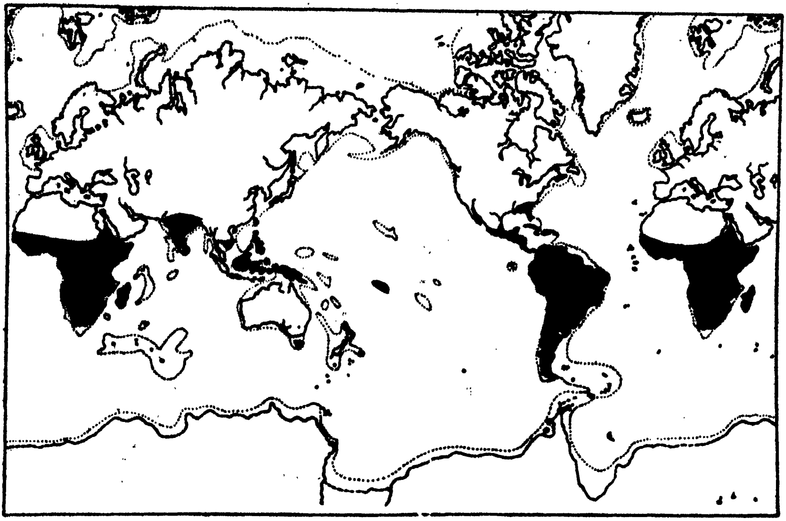

FIG. 10. DISTRIBUTION OF GASTROPHRYNIDAE.
The distribution of the genus *Calophrynus* (Madagascar, Burma, Borneo, Samoa) is of especial interest.

south-temperate lands, except for representation in India, southern China, Formosa and southeastern United States. They are hospitable to all genera of Opalinids, evidently adopting in any locality the Opalinids there present. I know of nothing in themselves or in their parasites to indicate northern origin and we have no significant data from fossil forms. The fact that two Gastrophrynids bear Opalinids apparently transitional between the genera *Protoopalina* and *Zelleriella* is an indication, of not too great weight, that they have lived for a goodly period in tropical America, the place of origin of the genus *Zelleriella.* The presence of a Gastrophrynid (*Calophrynus*) in Samoa and of an Australian Leptodactylid (*Limnodynastes*) in the New Hebrides is worthy of notice. The latter probably migrated eastward to its present island home. The Samoan Gastrophrynid may likewise have entered from the west.

Of the Bufonidae, the probably more modern genus *Bufo* (Fig. 11) is cosmopolitan, except for Australasia and Madagascar, one species (*Bufo dialopus*) being reported even from the Hawaiian Islands, though its being a native form has been questioned, the other, more archaic, genera (Fig. 12) are exclusively tropical. I know

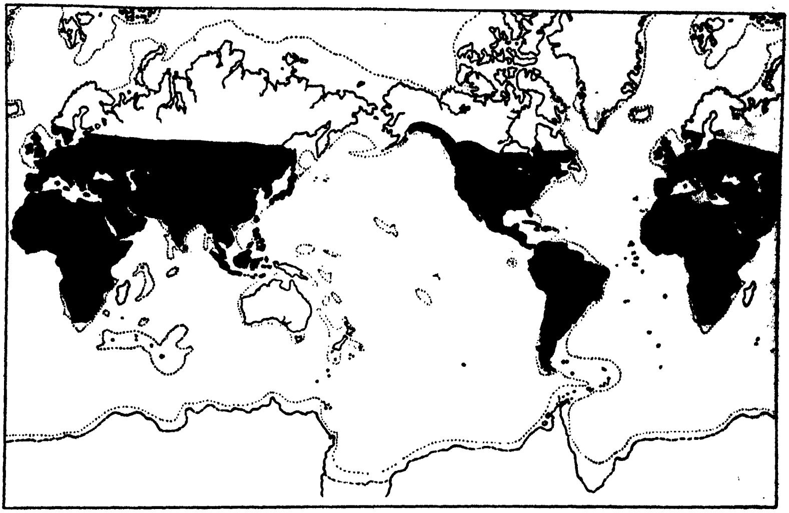

Fig. 11. Distribution of Bufo.

The report of a native *Bufo* (*dialopus*) in the Hawaiian Islands has been questioned.

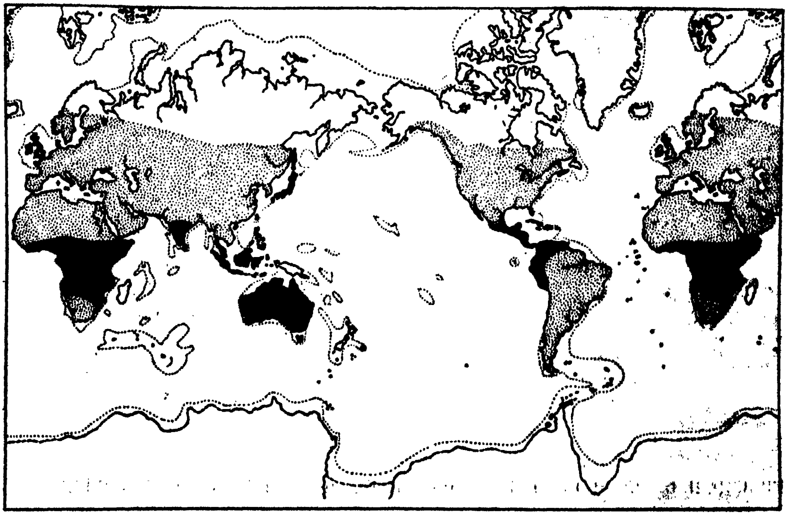

Fig. 12. Distribution of Bufonidae.

The presence of archaic genera is indicated in black. *Bufo* is found over all the stippled and the black areas except Australia and Tasmania. The report of a native *Bufo* (*dialopus*) in Hawaii is questioned.

of no indication that these more archaic Bufonids may have had a northern origin.[12] Fossil Bufonids are known from the early Tertiary of Arctogea, but these apparently are all referable to the genus *Bufo*. The Bufonidae, then, give no evidence in favor of Matthew's hypothesis. No more do their Opalinid parasites, for *Bufo* adopts any Opalinids present in its habitat, and other Bufonid genera may likely have the same habit. It is of interest to note that none of the Bufonidae of South America are found to carry any multinucleated Opalinids, though these occur in the Bufos of Central America and southwestern North America, indicating that probably Bufonids have not passed southward over the Isthmus of Panama since the entrance of the genera *Cepedea* and *Opalina* into southwestern Nearctica.

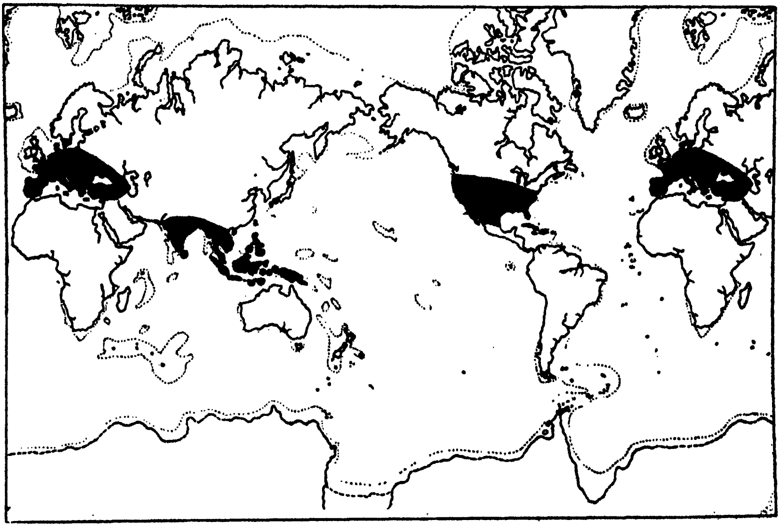

FIG. 13. DISTRIBUTION OF PELOBATIDAE.

The American Pelobatids are all of the exclusively American genus *Scaphiopus* ("Spade-foot Toads").

The Pelobatidae (Fig. 13), perhaps an offshoot from early ancestors of the Bufonidae, are to-day exclusively Arctogean, except that they have spread across Malaysia to Papua. Their Opalinids are of the archaic genus *Protoopalina*, except that in North America the endemic Pelobatid genus *Scaphiopus* has adopted also one *Zelleriella*, one, or possibly two *Cepedeae* and two modern narrow *Opalinae*. I have suggested the origin of the Pelobatidae in southeastern Asia soon after the separation of Australia from Asia at the beginning of the Cretaceous period (Metcalf, 1923).

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[12] *Eobatrachus agilis* Marsh is regarded doubtfully by Moodie (1912, 1914) as a Bufonid, possibly of the genus *Bufo*, but until its relationships are better understood it can hardly be taken into account.

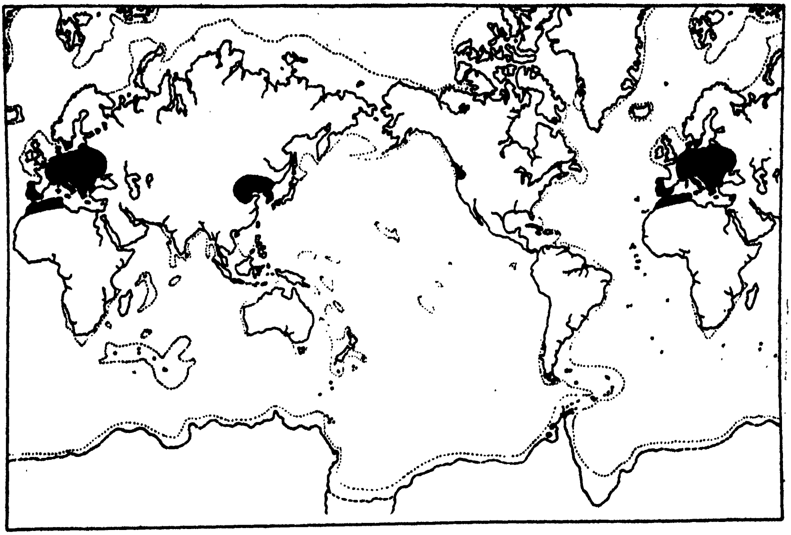

FIG. 14. DISTRIBUTION OF DISCOGLOSSIDAE.

On the western coast of North America, in the region near Puget Sound, is found *Ascaphus truei*, the only Discoglossid of the western hemisphere.

The Discoglossidae (Fig. 14) are northern to-day and I know of no indication in themselves or in their parasites to indicate the presence of members of this family at any time in the southern hemisphere. *Liopelma*, represented to-day by two species in New Zealand, was first described as a Discoglossid, but further study has resulted in assigning this genus to the family Leptodactylidae.

The Pipidae (Fig. 15) are probably among the more archaic of the Anura. They are now confined to the tropics, one subfamily, the *Xenopodinae*, in southern and

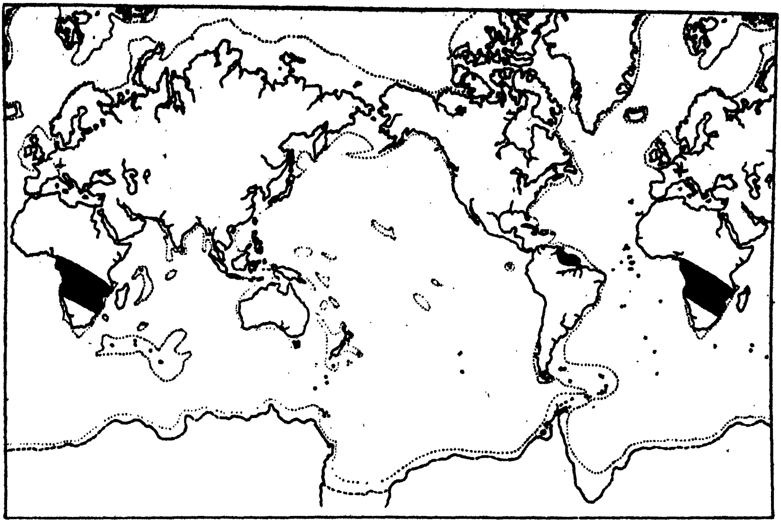

FIG. 15. DISTRIBUTION OF PIPIDAE.

In Africa *Xenopus* (2 species) and *Hymenochirus;* in South America *Pipa.* The presence of fossil *Palaeobatrachus* in Europe is indicated by a cross.

western Africa, and another subfamily, the *Pipinae,* in northern South America. Their known Opalinids are Protoopalinas of an archaic species reported only from Africa. One genus of Pipids, *Paleobatrachus,* was apparently abundant in Europe in Miocene times. The family arose probably several geologic periods earlier than this, for the Anura, from their present distribution, seem to have evolved at least as early as the Triassic period (Metcalf, 1923). If we regard *Pelion lyelli* as ancestral to the Anura, their evolution had begun in the Carboniferous period (mid-Pennsylvanian, Linton beds, of Ohio).[13] The extent of the distribution of the earliest Anura in pre-Triassic times is not indicated by fossil remains. Indeed we have no undisputed pre-Cretaceous remains of Anura.

Subfamilies whose parasites are unknown are not included in this discussion.

What, then, are the suggestions from this review of data?

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[13] See Moodie (1914).

(1) The Anura seem to have arisen in the earliest Mesozoic, or even in the Paleozoic era, but the extent of their dispersal in these early times is not indicated by evidence from themselves or their parasites (except in connection with paleogeographic data still *sub judice*).

(2) Some groups of Anura are now wholly or chiefly of northern habitat and may well always have been northern. Among these are the Archaic Discoglossidae, the Pelobatidae (a far from modern family) and the *Raninae* (a subfamily highly evolved and structurally comparatively modern, though fossil Ranas are known from strata as early as the Oligocene).

(3) One ancient group of Anura, the Pipidae, is now of southern habitat, but shows evidence from fossils of having once been also in the north.

(4) Other groups are now chiefly southern with some representatives in the southern edges of some Arctogean lands: Bufonidae (other than *Bufo*), Gastrophrynidae, *Raninae* (other than *Rana*), *Dendrobatinae,* Leptodactylidae. The southern genera of Bufonidae seem more archaic than *Bufo,* and the southern genera of *Raninae* seem more archaic than *Rana.*

(5) The Leptodactylidae, while well represented in Central America and present in Texas and the West Indies, are a southern family. They carry a southern Opalinid parasite (*Zelleriella*), and they seem never to have been in Euro-Asia, though found to-day in Australia, Tasmania, New Zealand, Papua and Erromango (one of the New Hebrides Islands). Their route of transfer between South America and Australasia seems to have been southern—probably by way of Antarctica during its period of mild moist climate in the early Miocene.

(6) The Hylidae, though represented to-day in Euro-Asia by half a dozen forms (perhaps one species with several subspecies) carrying modern Opalinid parasites of North American origin, are an American and Australasian family, apparently evolved in South America. Their route of migration between tropical America and

Australasia seems to have been southern, apparently across the Pacific Ocean and not by way of Antarctica, for they are not found to-day in southern South America or in New Zealand. The Samoan Gastrophrynid may have travelled by this same route, but whether eastward or westward is not indicated.

How do these data and conclusions fit with Matthew's and Dunn's theses?

Matthew No. 1 and No. 4: importance of climatic change as an influence upon distribution—not affected.

Matthew No. 2 and No. 7: principal lines of migration in later (including Mesozoic) geologic epochs radial from Holarctic centers of dispersal—opposed by the Hylidae and Leptodactylidae and their Opalinid and Trematode parasites.

Matthew No. 3 and No. 5: permanence of present oceans and no transoceanic bridges—opposed by the Hylidae and Leptodactylidae and their Opalinid and Trematode parasites.

Matthew No. 6: successive waves of migration from an evolution center, the more modern forms pushing the older forms toward the periphery—not supported by any of the Anura or their parasites, and opposed by some of the Anura. Note especially *Ascaphus truei* (Fig. 14), an ancient discoglossid, still present in the Olympic and Siskiyou Mountains, part of a generally accepted land strip between Asia and North America (Fig. 2). Instead of the more vigorous, modern forms pushing out the less vigorous, older forms, it seems that the more vigorous genera themselves spread over wide areas (*Rana, Bufo, Hyla*), while the less vigorous, perhaps diminishing in numbers, persist in their old habitats, in some cases aided by protective habits of seclusion (as, for example, the genera *Ascaphus* and *Scaphiopus* in North America, both sluggish species seemingly peculiarly defenceless), or by such special adaptations as the peculiarly disagreeable skin secretions of the Euro-Asian Discoglossid *Bombina* ("*Bombinator*").

In brief summary I would say that dispersal of land animals southward from Holarctic regions, especially into Africa, seems to have obtained in the later Tertiary, a period for which no southern intercontinental land-bridges have been postulated. It also seems evident that northward migration from South America took place in the latest Tertiary. Whether there were east and west migration routes between southern continents during the early Tertiary depends upon the date of such bridges. That they existed at some time seems indicated by the biogeographic evidence. When they existed, whether in Paleozoic and Mesozoic times only, or also in the early Tertiary, is still a mooted question.

Dunn's statement that the center of dispersal is best determined by the geographic center of the group range is too geometrical and too little biological, and could hardly apply to any family of Anura. Other data not conflicting, the region in which a family or subfamily is represented by the greatest number and variety of genera, or a genus by the greatest number and variety of species, is likely to have been inhabited by the group for a longer period than a region in which the group in question shows less divergent differentiation. But this latter suggestion does not seem to hold true without exception. Note the Hylidae, a family especially well adapted to the moist forests of tropical America. The largest number of its genera (subgenera) are in North America where the members of this tropical forest-loving family have spread to a region of greater variety of environment both climatic and physiographic. Animals are exposed to so varied and so intricate influences that their distribution can hardly be expressed upon geometric principles.

In all the above discussion I have followed the usually accepted conceptions of relationship among the Anura rather than Noble's (1922) more recent classification based partly upon the skeleton but chiefly upon the thigh musculature. I do not wish to express, nor even to exercise, independent judgment as to the general validity of Noble's classification, preferring to await further reaction from special students of the Anura. My only comment would be that Noble makes considerable and repeated use of the conception of parallel evolution in the cases of resemblance between animals living in widely separated habitats between which migration by routes available at present would be difficult to conceive. The outworking of parallel inherent tendencies in the evolution of divergent branches of certain Protozoan stocks (for example, the Ciliate parasites in the rumen of the Ungulata) seems clearly indicated, and in higher groups there are instances of parallel development of nearly related branches, but the conception is one to be invoked only with great caution and when the evidence from all sources seems quite clear. Its application to modern representatives of a conservative group of probably Paleozoic origin and of Paleozoic or Mesozoic differentiation calls for especially thorough scrutiny.

But whatever the result of further consideration of Noble's general taxonomic system, I find it peculiarly difficult to believe that, for example, the Leptodactylidae of tropical America and those of Australasia are not closely related genetically; and that similarly the *Zelleriella* parasites of the American Leptodactylids, almost, if not quite, specifically identical with the Zelleriellas of Australian Leptodactylids, are also the result of parallel evolution in the two continents; and that, at the same time, the Leptodactylid Trematoda of the two continents are closely similar because of a third series of parallel evolutions in these two regions of the Earth.

The possible alternatives also seem very difficult to accept:—either (1), *a,* of pre-Cretaceous presence in Arctogea of Leptodactylids, Zelleriellas and the special Trematoda characteristic of Australian and South American Leptodactylids and Hylids, *b,* of their pre-Cretaceous or early Cretaceous migration to Australasia and the American tropics,[14] and, *c,* of their complete suppression in the northern lands; or (2), *a,* of a later evolution of the three sets of forms, *b,* a late Tertiary migration to their southern homes, and, *c,* a complete disappearance from the north since, say, the middle Pliocene, the time of the establishment of the Isthmus of Panama (Vaughan, 1919).

The host-parasite evidence seems to me unassailable; multiple parallel evolution is not to be considered seriously. And the alternative assumptions, if we accept the host-parasite evidence and reject the idea of east and west migration routes in the southern hemisphere, seem more difficult than the hypothesis of former transoceanic bridges. It is somewhat interesting to note the somewhat general agreement of geologists, paleontologists and biogeographers as to the existence, general position and time of such intercontinental connections.

But perhaps the chief point of interest in such discussion as this is not any particular conclusion or any series of conclusions, but is, rather, the indispensable assistance of the host-parasite method in attack upon all such, and many other, problems. The host-parasite mine must be worked for all groups of animals and plants. Geologists, paleontologists, biogeographers, taxonomists and parasitologists must cooperate in the study of these problems, and the contribution of the parasitologists will not be the least important.

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# THE BEHAVIOR OF BLOOD-SUGAR VALUES IN HEREDITY

DR. OSCAR RIDDLE AND DR. HANNAH ELIZABETH HONEYWELL
CARNEGIE STATION FOR EXPERIMENTAL EVOLUTION

THE behavior in crosses of a character similar to or comparable with the normal sugar level of the blood has hitherto not been investigated. Earlier physiological work indicates that this is a character which is normally maintained at a given level throughout the whole of the life cycle so far as this has been studied; probably it is normally essentially constant for the species or race; in the individual it is much modified in certain diseases, and it shows very wide temporary fluctuations under a variety of external and internal conditions; finally, changes in blood sugar concentration are necessarily accompanied by other changes of concentration or of equilibrium not only in the blood itself but in the living tissues which must in turn equilibrate or adjust to changes in this circulating tissue. If, therefore, from a cross of different species or genera, a *hybrid* with a definitely new or different sugar level could be formed, all this hybrid's characteristics would be forced to undergo practically the whole of their development in an intimately surrounding medium different from that of its parents. Possibly we should thus have an opportunity to observe the response of the parental characters to this change (and doubtless of course to some or many other unknown or unstudied simultaneous changes) in the blood.

Studies on the inheritance of visible characters in crosses of widely separated forms—of distinct species, genera or families—have shown in some cases (Whitman, 15) marked irregularities and behavior of characters elsewhere known to segregate and show complete dominance or complete recessiveness. In other cases similarly wide crosses of other biological types have apparently failed to show notable departures from the expected behavior of these same characters. To us it seems probable that the results of the present study throw some light on the reason for the aberrant behavior of these visible characters in some generic crosses and also for the normal behavior of these same characters in other generic crosses. Whether justified in this speculation or not we are now able to establish one or two facts concerning the hereditary behavior of blood sugar values in two pairs of generic crosses.

The possibility of studying the behavior of blood sugar values in inheritance has only recently become apparent. This possibility has arisen in part through the fuller recognition and partial elimination of several factors which cause wide temporary fluctuations in the sugar values obtained from pigeons (6, 9, 10, 11, 12); and more important still from our demonstration (6, 9, 10) that different genera and families of pigeons—previously known to be fertile in crosses—have distinctly different normal levels of sugar in their blood. A fortunate aspect of those results presents itself in the circumstance that the two species of the two genera which previously had been most extensively used in genetic and sex studies by one of us were there shown to have almost the highest (*T. orientalis*; see Table II) and quite the lowest (*St. alba*) blood sugar values obtained from the several genera examined. And from this cross a sufficient number of $F_1$ hybrids and of $F_1$ back-crossed with one parent species were at hand for a partial investigation of this problem. From still another generic cross the two parents and 37 of their offspring supplied material for a second test.

## MATERIALS AND METHODS

After other studies had made it clear that, of the several species of pigeons studied by us, the Japanese turtle dove (*Turtur orientalis*) has almost the highest concentration of blood sugar and the ring doves (*Streptopelia alba* and *St. risoria*) have the lowest, it was decided to use all the adult hybrids of this cross then in our collection as the chief material of the present study. These hybrids were aged 17 to 183 months. From the 81 $F_1$ hybrids taken for study we obtained duplicate sugar determinations on 38 individuals which proved to be free of observable disease at autopsy. All the birds used in the study were killed after drawing the last blood sample to discover possible disease and to make sure that no ovulations were imminent in the females (6, 9). For hybrids other than the $F_1$ the available number of healthy individuals was considerably less—only 7 were "five eighths" Turtur hybrids; 8 were "one fourth" Turtur; 8 were either "one thirty second" or "one sixty fourth" Turtur and these are combined here and treated as one group. A study of a group of "one eighth" Turtur hybrids was delayed until after the onset of cold weather (October 19). Before this work could be carried out other studies had shown (11) that the blood sugar is considerably affected by the onset of cold weather in the autumn and the proposed study of this group of *Turtur* hybrids was therefore abandoned. The 10 *Turtur orientalis* and the 10 *Streptopelia* listed in Table I as "parent species" (all aged 10 to 47 months) are in most cases not the actual parents of any hybrids represented in the table; these hybrids arose from numerous matings of individuals of these genera, and in most cases the parents of the hybrids were not alive at the time this study was begun. The sugar determinations for the *Turtur* and *Streptopelia* "parents" and for the several groups of their hybrids were all made between April 28 and October 15. Except for a very few individuals this period ended on August 17.

A second group of $F_1$ generic hybrids—a large single fraternity from a cross of a *Spilopelia* male with a *Streptopelia* female—was also studied; and in this case the sugar values of the actual parents and of the fraternity of the female parent were determined. Autopsy showed, however, that only 20 of the 37 $F_1$ individuals from this generic cross were healthy; there being 7 tuberculous birds and 10 others infested with round worms. Several of these diseased birds gave very aberrant sugar values. The male *Spilopelia* parent was an imported (tropical) bird of uncertain age but certainly more than 3 years old and fully fertile in this generic cross. The female parent was 25 months old. Their hybrid offspring were all hatched in the same year and were aged 6 to 16 months when taken for this study. All the sugar determinations for all members of this group of birds were made between June 17 and August 17.

All the blood samples (except 12 *Streptopelia* and 12 *Turtur,* included in Figure 2, from samples obtained from the upper beak) were drawn by needle-puncture of the heart, and duplicate samples were taken usually at intervals of one day. The heart-punctures sometimes resulted in the death of the bird at the drawing of the first sample. This accounts for the "single determinations" separately listed for the $F_1$ hybrids in Table I. An examination of the distribution of deaths from nearly 1,000 heart-punctures indicates that death more frequently resulted in (a) diseased birds, and (b) in birds carrying eggs nearly ready to lay or to ovulate. The prevalence of disease in these birds and the questionable value attaching to an unchecked determination warrants our exclusion (or separate presentation) of the values thus obtained.

Since our earlier work (6, 9) has shown that the blood sugar increases in the female at the ovulation period, and since the heart-puncture was found occasionally to cause the resorption of an ovum in the ovary or to cause it to pass into the body cavity, it was necessary to obtain samples in females with resting ovaries and also necessary to autopsy the birds within one to three days of sampling in order to make sure that the ovaries were really resting. And since diseased birds should obviously be excluded, or be given separate consideration as is done here, it was necessary to kill the males also. It is of course only disease discoverable to us at autopsy that has been excluded, and probably a very few birds otherwise diseased are included in our groups of apparently healthy birds. Only non-ovulating sugar values enter into the data presented here. The sugar determinations were made by the Maclean micro-method. Further details of method, including precautions taken in the handling of the birds, have been described elsewhere (5, 9).

## DATA

Since the actual amount of sugar in the blood is subject to some fluctuation, notwithstanding the several precautions taken by us, and because of the small but appreciable error in the method of determination itself, and finally because any individual may have been significantly even though not discoverably diseased, it is usually necessary in a study of the present kind to attach more significance to results obtained for a *group* than to even well-checked results for an individual. This is a most serious limitation if the end in view were a complete and definite account of the behavior of a character in inheritance. But a thorough analysis lies wholly outside the scope of our purpose, since besides various limitations of method and material no $F_2$ generation can be reared from these generic hybrids, and we must deal chiefly with the $P_1$ and $F_1$ generations. We do, however, attempt a small amount of individual treatment of the data obtained from the two $F_1$ series studied by us.

Table I gives the details of results obtained from the various groups concerned in the cross of *Turtur* with *Streptopelia.* It will be noted that for 10 pure *Turtur orientalis* which proved healthy at autopsy we find 188 mgms sugar per 100 cc of blood. That this very high sugar value is not in excess of what we may accept as normal for this species is further indicated by the fact

## TABLE I

### SUMMARY OF BLOOD SUGAR DETERMINATIONS ON TWO PARENT SPECIES BELONGING TO DIFFERENT GENERA; ON THEIR MALE AND FEMALE $F_1$ RECIPROCAL HYBRIDS; AND ON HYBRIDS BACK-CROSSED TO ONE PARENT SPECIES

| Description of birds | | Sex | No. of birds in group | Average (or mean) | |
|---|---|---|---|---|---|
| | | | | Body weight | Milligrams sugar per 100 cc. blood |
| Parent species | Turtur orientalis | ♂+♀ | 10 | 221 | 188 |
| | Streptopelia alba-risoria | ♂+♀ | 10 | 171 | 149 |
| | All duplicate sugar determinations | | | | |
| One half T. orientalis ($F_1$) | Hybr. (♂ Turtur × ♀ Strep.) | ♂ | 17 | 199 | 174 |
| | | ♀ | 13 | 194 | 169 |
| | Hybr. (♂ Strep. × ♀ Turtur) | ♂ | 16 | 203 | 166 |
| | | ♀ | 19 | 184 | 158 |
| | Mean of 4 groups | | ...... | *195* | *167* |
| | All single sugar determinations | | | | |
| | Hybr. (♂ Turtur × ♀ Strep.) | ♂ | 4 | 191 | 150 |
| | | ♀ | 2 | 188 | 155 |
| | Hybr. (♂ Strep. × ♀ Turtur) | ♂ | 4 | 202 | 155 |
| | | ♀ | 6 | 187 | 163 |
| | Mean of 4 groups | | | *192* | *156* |
| | Healthy birds only and duplicate sugar determinations | | | | |
| | Hybr. (♂ Turtur × ♀ Strep.) | ♂ | 12 | 194 | 174 |
| | | ♀ | 9 | 197 | 169 |
| | Hybr. (♂ Strep. × ♀ Turtur) | ♂ | 9 | 204 | 165 |
| | | ♀ | 8 | 191 | 160 |
| | Mean of 4 groups | | | *196* | *167* |
| Five eighths Turtur orientalis[3] | | ♂ | 1 | 199 | 160 |
| (♀ 1/8 Turtur back-crossed with ♂ Turtur) | | ♀ | 6 | 203 | 174 |
| One fourth Turtur orientalis[3] | | ♂ | 4 | 170 | 164 |
| ($F_1$ back-crossed to ♀ Strep.) | | ♀ | 4 | 166 | 151 |
| Mean of 2 groups | | | | *168* | *158* |
| One thirty second or one sixty fourth | | ♂ | 2 | 171 | 164 |
| Turtur[3] (back crosses to ♂ and ♀ Strep.) | | ♀ | 6 | 155 | 151 |
| Mean[4] of 2 groups | | | | *163* | *157* |

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[3] Healthy birds only.

[4] The "mean" signifies the unweighted average of the two (or four) average values.

that 12 additional birds thought to be healthy, but too valuable to kill (used in Figure 2), gave a value of 190. And the seven additional diseased birds examined gave an average of 198 mgms; two of this group gave extremely low and four gave very high values. It has been shown by still other work that the ring doves (*Streptopelia*) are properly measured by the 149 mgms obtained from the 10 healthy individuals listed in Table I. This value is sufficiently confirmed by figures obtained for the two following groups: First, the 12 apparently healthy birds (too valuable to kill) added to the 10 known healthy birds in Figure 2; these gave an average of 150.6. Second, three small fraternities (parent and grand-parents) shown in Figure 3 gave a like result; only *Streptopelia* is represented there. The fraternity of the male grand-parent (*St. risoria*) gave a value of 152, the female grand-parent (*St. alba-risoria-douraca*), 148, and the parent fraternity, 147. These 14 *Streptopelia* again average 149 mgms sugar per 100 cc of blood. In a cross of these species of *Turtur* and *Streptopelia* it is evident that we are making a cross of sugar values which rather closely correspond to 188 and 149 respectively.

Three readily understood divisions of the data obtained for the $F_1$ hybrids are given in Table I. In each division four groups represent the necessary separations for the sexes and for reciprocal crosses. The third or last of these principal divisions should supply the most reliable results. It will be noted, however, that the larger numbers of (duplicate) determinations of the first division gives a result practically identical with that shown in the third division, although the first division includes a number of diseased birds. But the second group—including smaller numbers, unchecked determinations and a high proportion of diseased birds—gives values for both blood sugar and for body size which do not check well with the more complete and more reliable data. It is, nevertheless, notable that all of the four groups of this defective division, as well as of the eight groups of the two other divisions, *show a sugar value for the hybrids which is intermediate to those of the two parent species which entered the cross.* The mean value (167 mgms) obtained for the third (and first) division is an almost exact intermediate of the values found for the two parent species—being 21 points less than *Turtur* and 18 points greater than *Streptopelia.*

In a series of "five eighths" Turtur hybrids seven birds gave an average[1] value of 172 mgms. Thus, this group, which stands nearer pure *Turtur* in composition

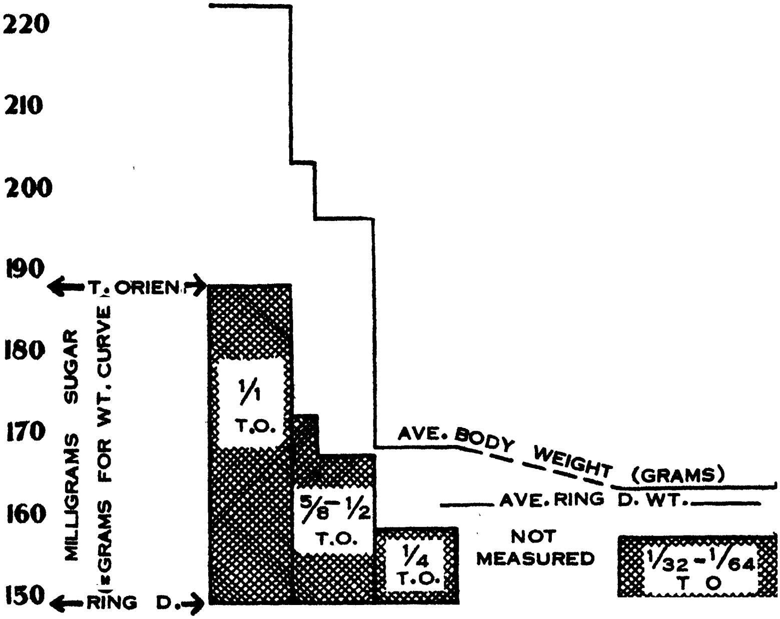

FIGURE 1

The rectangular blocks indicate the amounts by which the blood sugar values of *T. orientalis* and its various hybrids (five eighths; one half; one fourth; one thirty second) from crosses with the ring dove (*Streptopelia*) *exceed* the sugar value of the ring dove parent (the base line).

The uppermost line records the mean body-weight of the identical birds of the group whose mean blood sugar value is expressed in the rectangle below. The very similar and repeated "fractionations" of the body-weight and the blood sugar in the hybrids suggest that the same method of inheritance probably holds for both weight and sugar values.

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[1] The *average* is probably better used here than the mean, particularly since there is only one male, and since here only is the male indicated to have a lower sugar value than the female. In the case of all other hybrid groups the *mean* was used in the construction of Figure 1.

than do the $F_1$ hybrids, also more nearly approaches the sugar level of *Turtur* than do the latter hybrids.

The eight "one fourth" Turtur hybrids—arising from three different matings of $F_1$ hybrids ($F_1$ reciprocals both represented) back-crossed with *Streptopelia* females—again give a value (158 mgms) intermediate to that of their parents ($F_1$ and *Streptopelia*). The last class of these *Turtur* × *Streptopelia* hybrids—including eight birds which were only "one thirty second" or "one sixty fourth" Turtur—gave a mean sugar value of 157 mgms (average, 154) which is again an intermediate between the "one fourth" Turtur hybrid and the pure *Streptopelia.*

The above results are diagrammatically represented in Figure 1. The base line there represents the blood sugar level of the *Streptopelia* parents; and the shaded areas indicate the amount which this is surpassed, first by pure *Turtur* and later by the various hybrids of *Turtur* and *Streptopelia* in the order of their fractional or compositional relationship to *Turtur.* This diagram clearly indicates that the blood sugar value of the hybrids was "fractionated" or divided in the three (or four) graduated dilutions, or divisions, of the amount of *Turtur* represented in the offspring. If the reader wishes to visualize the total absolute sugar values of all groups, instead of their differences, he can do so by imagining the base line (149) carried downward at all points to zero.

A curve for the "body weight" of the several groups of birds which supply the blood sugar data is added to the uppermost section of the figure. This has been done to facilitate a comparison of the behavior of size and blood sugar in inheritance. The marginal figures which indicate "milligrams of blood sugar per 100 cc of blood" may be converted into "grams body weight" for the reading of this curve. In order to indicate the base of this curve, *i.e.,* the normal ring dove weight, we have not used the figure given in Table I for the 10 ring doves used there, but the value (161 grams) indicated by a much larger previous series covering the season at which the majority of the hybrids of this study were weighed and killed.

Since one would like to know something of the individual sugar values and the range of variation which gave the mean intermediate value (167 mgms) for the $F_1$ hybrids of this cross, we have supplied these data in the form of a polygon in Figure 2. This figure makes it clear that the mode of this polygon corresponds with the mean value (167 mgms; average, 166) and that our mean and average values are not derived from the combination of numbers obtained from a bimodal curve. In other words, the values obtained are distributed as are the values from characters which in $F_1$ show "intermediate" behavior in heredity. In order to have larger numbers of $F_1$ for this polygon, all the birds—including some unhealthy ones—of the first division of Table I are here utilized. And in order to have larger numbers for the construction of similar polygons for the two parent species we have here added to the 10 healthy individuals listed in Table I, an-

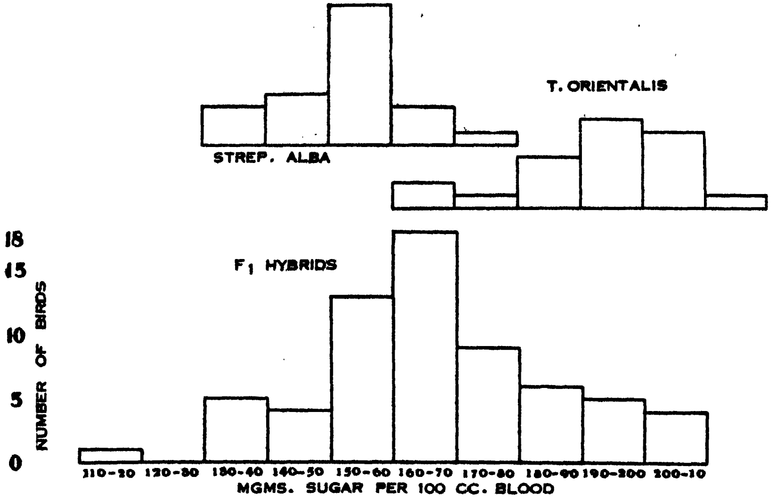

FIGURE 2

Polygons showing distribution of blood sugar values obtained from 65 $F_1$ *Turtur* × *Streptopelia* hybrids, and from 22 individuals of each of the two parent species (*Turtur orientalis* and *Streptopelia alba*).

other 12 individuals of each of these species which were all apparently healthy but too valuable to kill and verify this point. The polygon of each parent species therefore includes 22 individuals. The average blood sugar of the 22 *Streptopelia* represented is 151; of the 22 *Turtur,* 190. It is then also clear that these polygons for the parent species show a distribution about a single mode, and that this modal point includes the average blood sugar value found in the group as a whole.

The results obtained from a second generic cross—a male *Spilopelia suratensis* mated to a female *Streptopelia* hybrid—are diagrammatically represented in Figure 3. The blood sugar level of the *Spilopelia suratensis* is known only from the data obtained for the parent (♂ P870) used in this cross; but the value (170 mgms) obtained for this individual is the result of three well-checked determinations. One individual of another species of this genus—*Spilopelia chinensis*—gave 173 mgms sugar. The sugar value obtained for the female parent of the hybrids of the cross now being discussed requires special consideration.

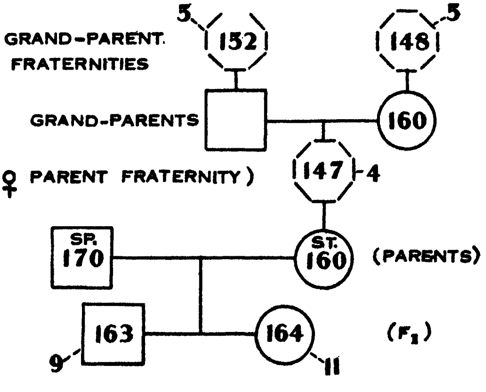

FIGURE 3

Family history, in terms of blood sugar values, of 20 (9 ♂ and 11 ♀) healthy generic $F_1$ hybrids and of their male (SP. 170) and female parents (ST. 160). These hybrids show an average and a mean sugar value intermediate to the values of their parents and of the genera to which their parents belong.

The blood sugar value given in Figure 3 for the female parent (P995) is 160 mgms. This is of course the value obtained; but the autopsy revealed that this was not a true non-ovulation value—an unsuspected ovulation into the body cavity having occurred about two days before the blood samples were drawn. Other work has shown (6, 9) that the sugar value increases at ovulation and that about 108 hours must then elapse before the blood sugar again returns to normal. Under these conditions the sugar value obtained was almost certainly too high. But we have the following evidence concerning the sugar value which she would be expected to transmit to her offspring: Sugar determinations made on four individuals of her own fraternity gave an average of 147 mgms; her mother gave a value of 160, but this also was probably abnormally high since five determinations on individuals of her own family (fraternity and parent) gave a value of 148 mgms; again, five members of her father's family gave a value of 152 mgms. The average for the 14 birds of her own fraternity and ancestry was therefore only 149 mgms sugar. This is exactly the value obtained by us for ring doves in general and is the probable value which female P995 would transmit to her offspring.

From the preceding data and discussion it may be concluded that in this second generic cross a sugar value of about 149 was crossed with another of approximately 170. The two groups of hybrids obtained—male and female—are both shown in Figure 3 to have had blood sugar values intermediate to those borne by their two parents. Apparently these values in the offspring are nearer to that of the *Spilopelia* parent; they would be exactly intermediate if the true blood sugar value of *Spilopelia* should prove to be about 178. Whitman (16) has shown that *Spilopelia* has a closer phylogenetic relationship to *Turtur* than to *Streptopelia* and this would lead to an expectation of a higher value than 170 in *Spilopelia* rather than of a lower value. And we have already noted that a single individual of *Spil. chinensis* gave a value of 173. Unquestionably both groups (males and females)

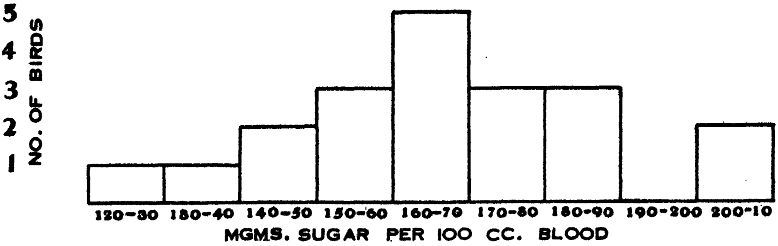

FIGURE 4

Polygon showing distribution of blood sugar values obtained from 20 healthy $F_1$ *Spilopelia* × *Streptopelia* hybrids.

of these hybrids have values distinctly above the known sugar values of *Streptopelia*; and they have a smaller value than that found for their *Spilopelia* parent.

It is of interest to note that the $F_1$ hybrids described above have a lower sugar level than have the hybrids from the comparable ♂ *Turtur* × ♀ *Streptopelia* cross shown in Table I—the males there giving 174 against 163 here; the females 169 there against 164 here. The *Turtur* parents of the earlier cross had a sugar value of 188, while the *Spilopelia* parent of the present cross apparently had a sugar value of only 170. Figure 4 supplies the evidence that the average values obtained here do not result from a combination of values from a bimodal curve. The polygon of distribution of the $F_1$ hybrids is again such as to indicate that the character crossed behaves as do intermediate or blending characters.

We have elsewhere (10) given full consideration to the question whether there is a sex difference in the blood sugar level in males and females of pure species. On the question of such a sex difference in hybrids we possess only the data presented above. The sex differences found in hybrids from the *Turtur* × *Streptopelia* cross are perhaps sufficient, if they stood alone, to suggest a higher value in the male hybrids. But the data for the *Spilopelia* × *Streptopelia* hybrids do not support this view and the point must be regarded as quite uncertain. Do the reciprocal hybrids have equivalent sugar values? On this matter also our data are all given here and the results from the single group thus tested (*Turtur* × *Streptopelia*) seem to indicate a higher sugar value in the hybrids when *Turtur* is used as the male parent. It is possible, however, that if duplicate determinations had been obtained from the 16 birds with unchecked determinations (second division of Table I) their checked values would have been quite close to those tentatively tabulated for them, and that significant differences for both reciprocal crosses and for sex in hybrids would thus be largely eliminated. Conclusions on these points can not now be drawn; but these possible differences are noted as the reason for using *mean* values instead of averages in dealing with the data of Table I. Fortunately, the mean and the average are almost identical for most of the groups represented in that table.

## DISCUSSION

The data of the present paper clearly indicate: (a) That in the two generic crosses made by us the blood sugar of the parent genera stood at distinctly different levels; (b) that the $F_1$ hybrids from both of these crosses had values intermediate to those of the parent genera; (c) that this intermediate value in the one tested case again divided or "fractionated" in a back-cross with one of the parent species; (d) and that in still other fractional parts of parental composition (five-eighths, one-thirty-second) there is found some evidence that the sugar level is either further divisible or that it still shows the presence and hereditary effect of both parental genera. The data are not of such nature as to test the question as to whether segregation does or does not occur and are otherwise obviously limited in amount and in their application. But the character here studied is a less superficial one than are the visible characters whose hereditary behavior have become well known, and the possibility of an influence of this more deeply-seated character upon those visible and more superficial characters is a point of interest.

TABLE II

APPROXIMATE AND COMPARATIVE AMOUNTS OF REDUCING SUBSTANCES IN THE BLOOD OF VARIOUS ANIMALS AND IN SEVEN GENERA OF PIGEONS

| Animal | No. of | | Reducing power of blood (milligrams sugar per 100 cc blood) | Observer |
|---|---|---|---|---|
| | Animals | Determinations | | |
| Man | ...... | 61 | 84 | Strouse |
| Horse | ...... | 2 | 70 | Abderhalden |
| Sheep | ...... | 2 | 70 | Abderhalden |
| Cat | ...... | 16 | 70 | Scott |
| Dog | ...... | 7 | 75 | Scott and Hastings |
| Rabbit | ...... | 25 | 118 | Scott and Ford |
| Duck | ...... | 14 | 150 | Kausch |
| Goose | ...... | 6 | 150 | Kausch |
| Fowl | ...... | 9 | 200 | Saito and Katayama |
| Tortoise | ...... | 4 | 90 | Bierry and Giaja |
| Frog | ...... | 26 | 40 | Scott and Kleitman |
| Dog-fish | ...... | 4 | 65 | Scott |
| Chimaera | ...... | ...... | 28 | Lang and Macleod |
| Cancer | ...... | ...... | 40 | Lang and Macleod |
| Octopus | ...... | ...... | 32 | Bierry and Giaja |
| VARIOUS GENERA OF PIGEONS | | | | |
| Zenaidura carolinensis | 2 | 5 | 257 | Unpublished |
| Turtur orientalis | 22 | 43 | 190 | Riddle and Honeywell |
| Leucosarcia picata | 1 | 5 | 190 | Unpublished |
| Common pigeon (Columba) | 11 | 22 | 185 | Scott and Honeywell |
| Common pigeon (Columba) | 37 | 103 | 181 | Unpublished |
| Spilopelia chinensis | 1 | 3 | 173 | Unpublished |
| Spilopelia suratensis | 1 | 3 | 170 | Riddle and Honeywell |
| Stigmatopelia senegalensis | 9 | 15 | 168 | Unpublished |
| Streptopelia risoria<br>Streptopelia alba | 22 | 36 | 151 | Unpublished |

The curve for "body weight" which accompanies the data for blood sugar in Figure 2 is so similar to the curve for the latter as to permit the inference that the mechanism for the inheritance of the one applies also to the other. It must be pointed out that among doves or other animals there is no direct relation between body weight and blood sugar level such as would naturally result in the parallelism seen in Figure 2. The species with the highest blood sugar shown in Table II (*Zenai-*

*dura*) is with one exception the smallest species represented in the table; the smallest species (*Stigmatopelia*) has, with two exceptions, the lowest sugar, etc. Nor within the limits of a dove species is there any definite relation between the body weight and the blood sugar. The multiple factor hypothesis is the rather widely accepted interpretation of the more usual behavior of "body size" in inheritance. This interpretation is supported in most studies of this subject by one or another amount of observable and measurable segregation. Whether segregation of blood sugar values actually occurs is, as stated above, a question not tested by our data; we may add, however, that we do not therefore assume that it does occur. On this point our own view is that it is fairly clear that the most fundamental characteristics or properties of living matter—irritability, respiration, contractility, growth, etc.—obviously do not segregate, and that a multitude of visible characters certainly do segregate. Whether the normal hereditary level of blood sugar goes with the one group or with the other is quite unknown. The relatively large rôle of three to several glands of internal secretion, and of a part of the nervous system, in the normal maintenance and regulation of the blood sugar level would seem, however, to afford a logical basis for the assumption that the blood sugar level may have a "multiple factor" basis and that some or many of these factors may be segregable.

A few available observations bear in some degree on the point just mentioned. Pike and Scott (8) have called attention to the fact that a mechanism for maintaining the constancy of the sugar of the blood is one of a number of internal adjustments which the progressively higher animals have had to develop in greater and greater perfection. And Scott (14) has further suggested that in higher animals a delicate secondary mechanism has been developed and passed on through inheritance which permits a rapid variation of the blood sugar about the species norm as an emergency means of securing a prompt release of energy. All of these considerations emphasize the fact that the sugar of the blood is both a regulated and a regulating mechanism; and that its changes—whether of permanent or temporary nature—are of much greater significance to cells and tissues generally than are changes in the ordinary visible characters with which our studies of inheritance commonly deal.

It was noted at the beginning of this paper that studies on the inheritance of characters comparable with blood sugar values have not been made.[2] In this connection it should perhaps be remarked that the behavior of starchy and sugary characters—which are really alternative forms of the same thing—have received much attention in plant genetics. In maize crosses, for example, the chief facts for starchy and sugary endosperm have been reported by Correns (1), East and Hayes (2) and others. A paper by Pearl and Bartlett (7) supplies quantitative determinations of starch, various sugars, moisture, etc., in $P_1$, $F_1$ and $F_2$, from a one-direction cross made with two varieties of corn. In all the above work with maize a segregation of these sugary and starchy characters is shown to occur in the $F_2$. The $F_1$ endosperm of corn is of course not wholly comparable with the $F_1$ of the corn plant nor of the $F_1$ animal organism. The results of none of these studies seem really comparable with a character such as the blood sugar which, in the animal body, is under continuous regulation and whose temporary or permanent fluctuation in the circulating fluid calls forth other equilibrium changes in both the blood and in all tissues supplied with blood. That such equilibrium changes or adjustments on the part of blood and tissues accompany the permanently high or low sugar level follows necessarily from the general physico-chemical relations involved. But a special consideration of some aspects of these adjustments to altered concentrations of the blood sugar has already been supplied by Epstein (3) and by Woodyatt (13, 17).

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[2] Since 1920 our colleague, Dr. J. Arthur Harris, has been conducting extensive investigations on the physico-chemical properties of the tissue fluids of Egyptian and Upland cotton, and of their hybrids, as grown under irrigation agriculture at the Cooperative Testing Station, U. S. Department of Agriculture, at Sacaton, Arizona.

The blood change found and described by Gerould (4) in blue-green caterpillars is a quite different matter from the subject under consideration but may be briefly mentioned here. In this case the mutational character involved the destruction or decolorization of xanthophyll in its passage through the intestinal epithelium. As a result of this destruction the caterpillar's blood was free of the pigment, and all the various parts of the animal's body which were normally pigmented with xanthophyll through the blood supply were left without this pigment in all stages of the life-history of the insect.

The foregoing results lead to the suggestion that the intermediate blending or divisible nature of such characters as the blood sugar level in the $F_1$, and a second divisibility in the $F_1$ back-crossed to a parent genus, affords a possible explanation of some observed irregularities in the behavior of visible characters in wide crosses as this has been observed particularly by Whitman (15). Wide differences of such a character as blood sugar may usually be expected only in forms rather widely separated phylogenetically. That this is true in the case of blood sugar itself is indicated by the data assembled in Table II. From crosses of different genera of pigeons—where fertility extends even to different families—Whitman observed a number of phenomena which it is of interest to review in the light of the facts given above.

The final chapter of the second volume of Whitman's studies is devoted to a consideration of "The divisibility of characters." It was there shown that the $F_1$ obtained from crosses of wild species and genera of pigeons exhibit (sex limited characters partially or largely excepted) a blending of the parental characters. Moreover, the back-crosses of these $F_1$ hybrids again show a second or even a third "division" of the parental characters. Involved in these cases were such characters as general body coloration, the "neck-mark" as a whole, and both the coloration and bifid condition of the individual feathers within this neck-mark. We may note here that the analysis of the divisibility of the blood sugar level observed by us in the *Turtur* × *Streptopelia* cross quite closely parallels the behavior of the visible characters of these same hybrids as studied by Whitman. Again, our second case (*Spilopelia* × *Streptopelia*) involves the identical cross in which Whitman has described (15; see plate 34) a second "division" of the three above-mentioned characters of the neck-mark. Hereditary behavior of the above kind Whitman called "pure or direct inheritance."

A second type of irregularity of hereditary behavior encountered in these crosses of different genera by Whitman is concerned with the impurity or incomplete dominance or recessiveness of characters, notably of color characters; this being sometimes found even in cases of sex-limited color inheritance. For example,—in the very same birds used as principal material for the present study—the white color of *Streptopelia alba* never emerges even approximately pure white from crosses with *Turtur,* but shows various areas of partial pigmentation. These cases could also of course be "described" in terms of multiple factors, modifying factors, contamination, etc. The possibility that unequal numbers of chromosomes are contributed by these genera might also be considered. The results of this study, however, raise the question: Are the new and different levels of blood sugar—and of other similar though as yet unstudied elements introduced into the hybrid by wide crosses—perhaps these modifying or contaminating factors? The new and different blood sugar level of the hybrid certainly provides a somewhat different internal environment in which the characters proceeding from the parent forms must develop. Is no mark left upon the multitude of visible characters which must undergo the whole of their development under this new, persistent and intimate environment?

Still a third large group of cases of aberrant developmental or hereditary behavior is encountered among the hybrids proceeding from many wide crosses. The exhibition of fertility in all degrees and the fixed or limited life-terms of offspring in some of these crosses constitute one group of such characters; and the greatly increased frequency of reproductive abnormalities and of absent gonads in these offspring supplies us with another.

In none of these cases cited above is it necessary to suppose that an altered sugar level alone, nor that an alteration of any other single one of the several invisible characters which probably share the blood sugar mode of inheritance, is the sole cause of the aberrant behavior. The important point would seem to be that a new internal (blood) environment is established in such hybrids and that the parental characters show a developmental response to this new environment. We have here been able to show that one important element of such a new blood environment does occur in some of these hybrids; and we have noted that some of the characters of these same hybrids show atypical or unexpected hereditary behavior. Elsewhere we have shown (10) that the normal sugar level extends throughout the life cycle in the pigeon, and is already present in the embryo.

At the beginning of this paper it was noted that from some reported crosses of species or of genera there result, apparently, no notable departures from expected hereditary behavior. We are now able to offer a possible explanation for the issuance of normal hereditary behavior from certain wide crosses and abnormal or unexpected behavior from certain others. For, in some such crosses the blood sugar level—and other similar regulating characteristics of the blood or internal environment—may not be notably different in the forms crossed;

while other crosses do involve wide differences in these characteristics of the internal environment. In these latter cases the continued "fractionation" of such characteristics of the internal environment assists in the continued blending or fractionation of characters in the hybrids of the various grades. It is thus made evident that in the case of some wide crosses an agency for the modification of developing characteristics may come into action which is necessarily absent from crosses of closely related races, varieties and species.

On the basis of the facts obtained from the present study of the blood sugar of dove hybrids it is reasonable to assume that there exist other as yet unstudied characteristics of the blood—or internal environment—which behave in inheritance in the same way as does the blood sugar level. Some of these characteristics, states or processes may affect developmental processes more readily than do others. We venture the suggestion that some or many of the visible characteristics of two parent species which have developed in, and are presumably perfectly adapted to, a blood environment at one level may exhibit a response of one or another grade when forced to develop in a different blood environment in the soma of the hybrid. If this is true we are in a more favorable position to interpret some of the hereditary and developmental phenomena presented in hybrids from wide crosses.

## SUMMARY

The genera *Turtur* and *Streptopelia* were observed to have quite different amounts of sugar in the blood—respectively 188 and 149 mgms sugar per 100 cc of blood—and a study was made of the amount of blood sugar in various grades of hybrids of these two genera. A study of $F_1$ hybrids of a *Spilopelia* × *Streptopelia* cross was also made.

The $F_1$ hybrids obtained from both crosses had blood sugar values intermediate to those of the parent genera.

The offspring of $F_1$ hybrids of *Turtur* × *Streptopelia* back-crossed to *Streptopelia* again gave sugar values intermediate to those of the $F_1$ and *Streptopelia.* Still other grades of these hybrids obtained from back-crosses apparently also show a further blending or "fractionation" of this character.

The blood sugar level is apparently inherited in the same way as is body size in these same animals.

The behavior in inheritance of a character comparable with the normal blood sugar level has hitherto not been studied. The hybrids examined had a blood sugar value different from the values of the parent genera; this different value is maintained throughout the life cycle of the hybrid; and this different sugar value requires equilibrium adjustments on the part of other blood and tissue components of the hybrid in all or nearly all stages of the development, growth and life of the hybrid.

It is suggested that certain irregular and other little known hereditary or developmental phenomena often met with in hybrids proceeding from wide crosses are the result of the circumstance that in such hybrids the parental characters are forced to undergo the whole of their development in blood which constitutes a new, intimate and continuously acting internal environment.

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# EXPERIMENTAL ACCURACY IN FRUIT BREEDING

WALTER SCOTT MALLOCH
UNIVERSITY OF CALIFORNIA

PRIOR to 1900, pomological crops were bred and improved like other agricultural crops in a more or less empirical manner. The awakened interest in a more thorough investigation of pomological plants subsequent to 1900 is reflected in the statement made by U. P. Hedrick in regard to grape breeding. "The ultimate aim in this work is, of course, the production of improved horticultural varieties. Through the early days, when breeding laws and methods were less understood than now, there was a tendency to make this the immediate as well as the ultimate aim. The fact that the first twenty years of grape breeding produced but one variety worthy a name served to confirm the conviction that this goal would be reached quicker by forgetting it for the time being and bending every effort to the discovery of how grape characters are transmitted."

The importance to agriculture of accurate fruit breeding experiments may be illustrated by a single example. Among peach varieties there are those which are characterized by a considerable amount of anthocyanine pigment in the twigs, while others lack this coloring matter and hence have green twigs. The colored varieties absorb considerable heat and during the warm periods in spring the buds begin growth and hence are liable to injury during subsequent cold periods. Since the green twigged sorts are not subject to this type of injury they are more desirable in localities where cold periods occur during the year. The green twigged types have been found wild in the southern mountains and have a poor quality of fruit, while the colored forms include most of the commercial varieties. The recombination of such desirable commercial characters will be of great significance to horticulture. The employment of the proper breeding experiments is essential in the creation of such varieties. For example, if the green twigged character is recessive it would be necessary to raise the second generation and to control the pollination of the $F_1$ trees from which the second generation was obtained. Since this problem is the subject of investigation of another experiment station, I have referred to it as an illustration only in a very general way.

The analysis of the inheritance of characters in such large perennial plants requires a considerable period of time as well as a large expenditure of funds. For this reason genetic investigations with pomological plants have not made the same advances as such investigations in shorter life cycled plants. With the exception of such phenomena as bud mutations, senility and extended studies of hybrid vigor, fruit plants do not offer the most favorable material for genetic investigations. Such investigations have more of a utilitarian object than a scientific one in view. Due to this fact many of the tests performed in a genetic analysis may have to be omitted, but a classification of the particular phenotypes which are grown might be of considerable value in further breeding experiments. Though this is true, it should not alter the accuracy employed, but on the contrary, one would naturally suppose that, in breeding forms so costly in time and resources, the most exacting technique would be one of the first essentials.

The greatest advances in any of the commercial fields have resulted from the utilization of scientific discoveries. This will be true in pomology and any agricultural field as well as in chemistry or engineering. Disregarding the question of methods to employ in commercial breeding the criticisms in this paper are justified because the articles reviewed purport to give a genetic classification and interpretation of certain fruit breeding experiments. In looking over the breeding literature along pomological lines, one is usually impressed by the inaccuracies of an experimental nature and the misinterpretations which are employed.

One of the first prerequisites for the establishment of accurate genetic facts or for the isolation of desired recombinations is the use of sufficient numbers. The employment of a number of crosses with a few individuals each is one of the commonest failings of fruit breeders. If any genetic experiment requires large numbers an investigation of horticultural plants certainly would because of the heterozygosity of many of the varieties.

Babcock and Lloyd (1917) have pointed out that the restriction of the use of scientific terms to a given set of conditions is necessary for mutual understanding. Likewise the discussion and interpretation of genetic data according to logical scientific reasoning is equally essential to mutual understanding. In the remainder of this article I will try to point out a few of the inconsistencies of this nature which have occurred in fruit breeding literature within the last few years.

Hedrick and Anthony (1915) crossed grapes having abortive pollen and normal pistils with those having normal pollen and rudimentary pistils. From this cross they obtained 56 hermaphrodites and 51 with rudimentary pistils. When perfect hermaphrodites were selfed only perfect hermaphrodites were obtained. Vines with abortive pollen were referred to as hermaphroditic females and forms with rudimentary pistils as pure males. The discussion of the inheritance of these forms was referred to as a case of sex inheritance. They state that

> this condition might be covered by the assumption that the hermaphrodite is a female in which the addition of a single dose of maleness has caused the production of male organs, the ovules keeping the composition ♀ ♀ and the pollen becoming ♂ ♀.
>
> Hermaphrodite × hermaphrodite = ♀ ♀ × ♂ ♀ = 2♂ ♀ + ♀ ♀.
>
> Since we have no pure females, we must assume that some condition prevents the formation of individuals with the composition ♀ ♀; therefore, the above cross gives only hermaphrodites. Of course, if we do not attempt to assume the method of origin of the hermaphrodite, the case may be covered by considering the hermaphrodites pure for this character, while the males would be heterozygous.
>
> ♀ ♀ × ♀ ♀ = ♀ ♀
> ♀ ♀ × ♀ ♂ = ♀ ♀ + ♀ ♂.

The misconceptions of this explanation are evident to any one who is familiar with modern cytology. If we take their statements literally they assume a diploid condition instead of the haploid condition for the ovules and pollen. If one interprets their statements to mean that the ovules of hermaphroditic vines are all of one kind, let us say the X type, and the pollen of the same vine is of two types as X or Y, then we must devise some mechanism by which this could take place. Since their explanation is entirely inconsistent with present knowledge we would have to reconstruct a hypothesis based upon some of the known facts of sex inheritance in plants if their observations are to be included in this category. Their data, however, are not sufficient to justify anything except a purely speculative theory, and it will be pointed out in the following paragraph that the case can be explained without involving sex inheritance.

White (1914) has demonstrated that petalody and pistillody of the anthers of tobacco flowers are inherited characters. Since factors are known which cause teratological structures to develop on anthers it would be logical to assume that there might be factors which cause the suppression of pollen or pistils in grape vines. We could assume a recessive inhibiting factor (s) for pollen development and a recessive inhibiting factor (p) for pistil development. If the vine with defective pollen was represented by the formula Ppss and the vine with rudimentary pistils by ppSS, then the progeny from an immediate cross between these vines would be of two kinds, PpSs or perfect hermaphrodites and ppSs or vines with rudimentary pistils and these two types would occur in equal proportions. The correct explanation of the inheritance of defective sex organs in grapes will, of course, depend upon further breeding data. It is sufficient to point out that Hedrick and Anthony are not justified in their assumption of sex inheritance in grapes without further breeding tests.

The statement by Connors (1919) in regard to the inheritance of flesh color in peaches is even more inconsistent. "Since most of our peach varieties are chance seedlings, we do not know with any certainty what these varieties carry as recessives in flesh color. An example of this is the variety Elberta. This variety is known to be a seedling of Chinese Cling. If Chinese Cling were pure white and were crossed with a yellow variety then all the seedlings in the $F_1$ generation should be white, unless color of flesh is a sex-linked character." Peaches are a hermaphroditic species and hence sex-linkage is not possible according to the way this term is used by geneticists.

But the misuse of genetic terminology is not the greatest sin committed by fruit breeders. The accompanying table taken from Connors (1919) lists inconsistent reciprocal crosses without stating whether the same trees were used for these reciprocal crosses. This criticism is justified from the looseness in which other genetic terminology has been used in the same article. Reciprocal may have been used simply in the sense that the same varieties were employed. In order to have a reciprocal cross when working with fruit varieties, identical trees must be used in both crosses unless it is accurately known that another tree of the same variety was propagated from a second cutting of the bud wood from which the first tree came. In this connection it is sufficient to point out that in many orchards the trees have not been obtained from the same nursery. The present pomological varieties include trees of different origin and hence of possible different genetic constitutions. An inspection of Table III of his article indicates at once that there is something wrong with the reciprocal crosses. The fact that the two crosses, one involving Early Crawford × Belle and the other Early Crawford × Elberta, both gave inconsistent reciprocal results would throw doubt upon the Early Crawford parent which was used in these reciprocal crosses. A statement as to the identity of the parents would have been of great aid in the interpretation of the results.

Furthermore, the table shows that the results of two distinct crosses are added together for a total. This practice has been followed in a second publication dealing with the same fruit (Connors 1921). Such a procedure would have significance provided that it was previously demonstrated that Belle and Elberta carried identical genes for size of flower, but this was not done.

TABLE III[1]

| | Large | | Medium | | Small | | Total |
|---|---|---|---|---|---|---|---|
| | No. | Per Cent. | No. | Per Cent. | No. | Per Cent. | |
| Belle × Early Crawford | 1 | 0.8 | 76 | 63.3 | 43 | 35.8 | 120 |
| Elberta × Early Crawford | 11 | 14.1 | 46 | 59.0 | 21 | 26.9 | 78 |
| Totals | 12 | 6.1 | 122 | 61.6 | 64 | 32.3 | 198 |
| Early Crawford × Belle | ...... | ...... | 21 | 80.8 | 5 | 19.2 | 26 |
| Early Crawford × Elberta | ...... | ...... | 21 | 50.0 | 21 | 50.0 | 42 |
| Totals | ...... | ...... | 42 | 61.8 | 26 | 38.2 | 68 |

In another publication Connors (1921) described the seedlings grown from self-fertilized seeds of trees having reniform glands on the petioles and margins of the leaves. All of these varieties produced seedlings having leaves with reniform glands. Several of the varieties with reniform glands were crossed. Most of the crosses gave seedlings, all of which had reniform glands. One cross, however, Slappey × Arp, gave 23 seedlings with reniform glands and 6 with globose glands. This result is explained by the following statement. "It is possible that accidental mixture has taken place in this instance either at the time of harvesting the seeds from which the trees came, or in planting the trees in the orchard, because the six with globose glands resemble closely the seedlings from Slappey × Early Crawford." The publication of all the data of any experiment whether it conforms to expectation or not is highly desirable and small errors do occur occasionally in experimental work. The occurrence of such results as given by the cross Slappey × Arp could easily be due to the interaction of factors or to some similar genetic reaction. Nevertheless, the sentence would seem to indicate a lack of accurate control of experimental material, a very common error in so-called commercial experiments.

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[1] Large, medium, small refer to size of peach flowers. Early Crawford had small flowers while Belle and Elberta had medium sized flowers.

Beach and Maney (1912) have reported upon a cross between the western sandcherry (*Prunus besseyi*) and the Wyant plum (*Prunus americana*). "Number of serrations.—As a result of numerous measurements serrations to the inch averaged 9.7 on the sandcherry and 12.6 on Wyant. The classification follows. The results are inconclusive."

| Group | Number | Per cent. |
|---|---|---|
| 1 | 14 | 11.2 |
| 1a | 29 | 23.2 |
| 2a | 37 | 29.6 |
| 2 | 45 | 36.0 |
| Total population | 125 | |

It followed from previous explanation that the results tabulated were for the second generation and that the group classification had the following significance.

1 Individuals most closely approximating the type of the mother $P_1$.
1a Intermediates which most favor the mother type $P_1$.
2a Intermediates favoring the male parent $P_1$.
2 Individuals most closely approximating the type of male parent $P_1$.

Since the above quotation includes all the data which the authors present on the inheritance of number of serrations, one has no way to judge as to how clearly the different groups were separated from one another or in what manner the data were treated. Since the authors tabulated intermediate types and since number of serrations would probably be a quantitative character, the data should have been treated as a frequency distribution rather than an arbitrary classification into four different groups.

It is needless for the purpose of the present discussion to multiply examples of errors which have occurred in publications of several fruit breeders within the last few years. Similar flaws could be pointed out in some other types of pomological investigations of recent date. It would likewise be more useless to attempt to revise this literature since the data in most cases have not been presented in a form which can be interpreted. In most articles where the data are presented in a form which can be checked easily, the conclusions are stated equally well.

One may conclude by saying that the analysis of the hereditary constitution and the improvement of fruit plants offer a unique field for the trained investigator as well as being of great importance to agriculture. It seems almost a tragedy, however, to expend a great amount of time and funds for inaccurate investigation when accurate results could be secured equally as well.

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# YELLOW FEVER AND FISHES

PROFESSOR C. H. EIGENMANN
INDIANA UNIVERSITY

CONSIDERABLE interest has developed in Ecuador and Peru by utilizing fishes to control yellow fever. Various fevers are communicated from person to person by the bite of various mosquitoes. No mosquitoes, no fever.

Any means that will suppress mosquitoes will suppress fevers. There are three ways to eradicate mosquitoes. Abolish the breeding places of mosquitoes. This is easier said than done. A swamp may be drained, but a tomato can or two left exposed to rain is sufficient to interest a whole neighborhood. It has been reported somewhere that a poverty-stricken college complained to a proverbially rich factory owner that his pond adjoining the college grounds was a mosquito nuisance. He offered the college a dollar for every mosquito larva caught in his pond. The students turned out in mass to catch mosquito larvae and earn dollars. But they did not earn a dollar because it was discovered that an old posthole on the college campus was providing the mosquitoes. Considerable energy has been spent draining swamps to get rid of the breeding places of mosquitoes.

The suppression of mosquitoes by oiling the surface of all standing water was the classic means employed in Panama.

It has been known for years that some fishes make away with some mosquito larvae. Probably most young fishes eat mosquito larvae. Some fishes are more effective mosquito larva eaters than others. It is current belief that the "millions" of Barbadoes, *Acanthophacelus reticulatus* (also native in Trinidad and along the lowlands of the Guianas) have kept yellow fever out of Trinidad.

In North America Gambusia plays the principal rôle as a mosquito eradicator, and extensive plans are carried out by S. F. Hildebrand of the Bureau of Fisheries to distribute Gambusias to places where they are most needed and where they will do the most good.

Within the last few years, experiments were made near the coast of Ecuador and Peru to find mosquito eaters among the native fishes.

To serve as an ideal yellow fever mosquito larva eater, the fish must not only eat larvae, but it also must be able to live under the conditions in which yellow fever mosquitoes breed. Yellow fever mosquitoes live about and in the houses of man. They breed in the various water jars, cans and barrels in which drinking water is stored. The fishes, therefore, must thrive in standing water. "Millions" were imported for the larger containers in Guayaquil and the following three native fishes, named in the order of their importance, were found to best serve the purpose of removing mosquitoes from houses.

1. The most important is "Life" (Fig. 1) (*Pygidium piurae* E.), a small catfish belonging to a South American family of about 100 species. The genus Pygidium embraces over half, (sixty-five) of the known species. The different species differ but little in habit and appearance and probably all of them will serve as mosquito larvae eaters. They are found in all of the mountains of South America from the edge of Panama, at least to Puerto Montt in Chili. They have been caught from sea level all the way to 12,000 feet and more. They are hardy mountaineers lying at the bottom of torrents in daytime, coming to the surface at night to feed.

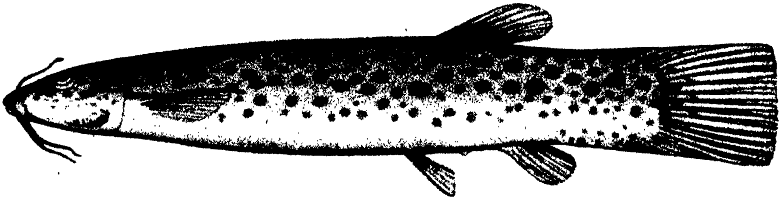

FIG. 1. "Life," Pygidium piurae E.

The map (Fig. 2) shows the general distribution of members of the genus Pygidium. I found a few about

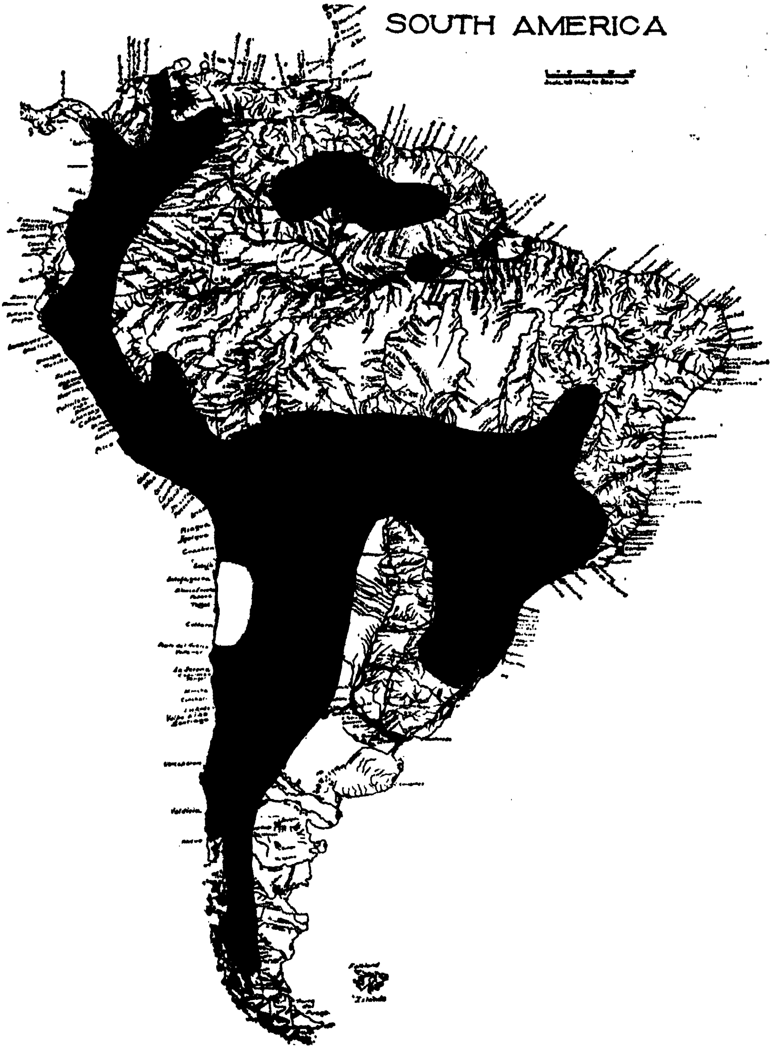

Fig. 2. Distribution of the genus Pygidium. They are most abundant in the cooler mountain streams. A very small species is found at the bottom, even burrowing in the hot Amazon Valley.

the cataracts in British Guiana and have put a hypothetical island, I, covering the highlands of the Guianas in the Pygidium-free lowlands. Similarly, a minute species has been recorded from II in the Amazon and it is possible that they are found throughout the Amazon Valley.

Without doubt their most extensive habitat is along the slopes of the Andes and in southeastern Brazil. Actually no Pygidium has been recorded south of Puerto Montt where they are still found in great abundance. South of that point members of a closely related genus (Hatcheria) have been recorded.

Eight hundred thousand of "lifes," distributed to all of the water jars in the infected regions by Dr. H. Hanson, suppressed the last yellow fever epidemic in Peru.

The distribution map is a modification of one prepared for my monograph of this family. "The Pygidiidae" (Mem. Carnegie Museum VII, 1918, pp. 259-397, plates XXXVI-LVI).

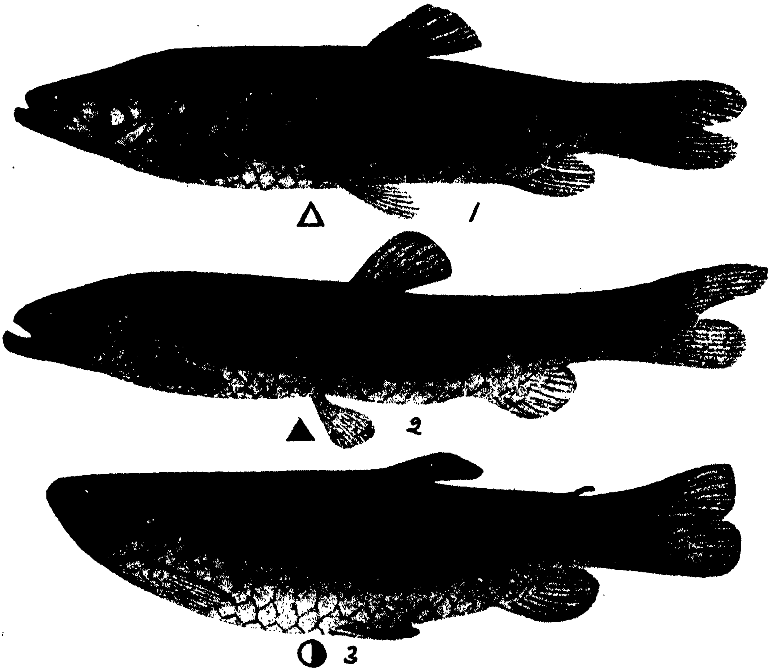

Fig. 3. The "Huaija," *Lebiasina bimaculata*, its nearest relative *L. multimaculata* and a more remote relative *Piabucina panamensis*.

2. Liza de agua dulce of Lima and Huaija of Guayaquil are different names for the same fish—*Lebiasina bimaculata* (Fig. 3). This is a very active fish. It was independently discovered to be a larva eater by Dr. W. Pareja in Ecuador and by H. Hanson in Peru.

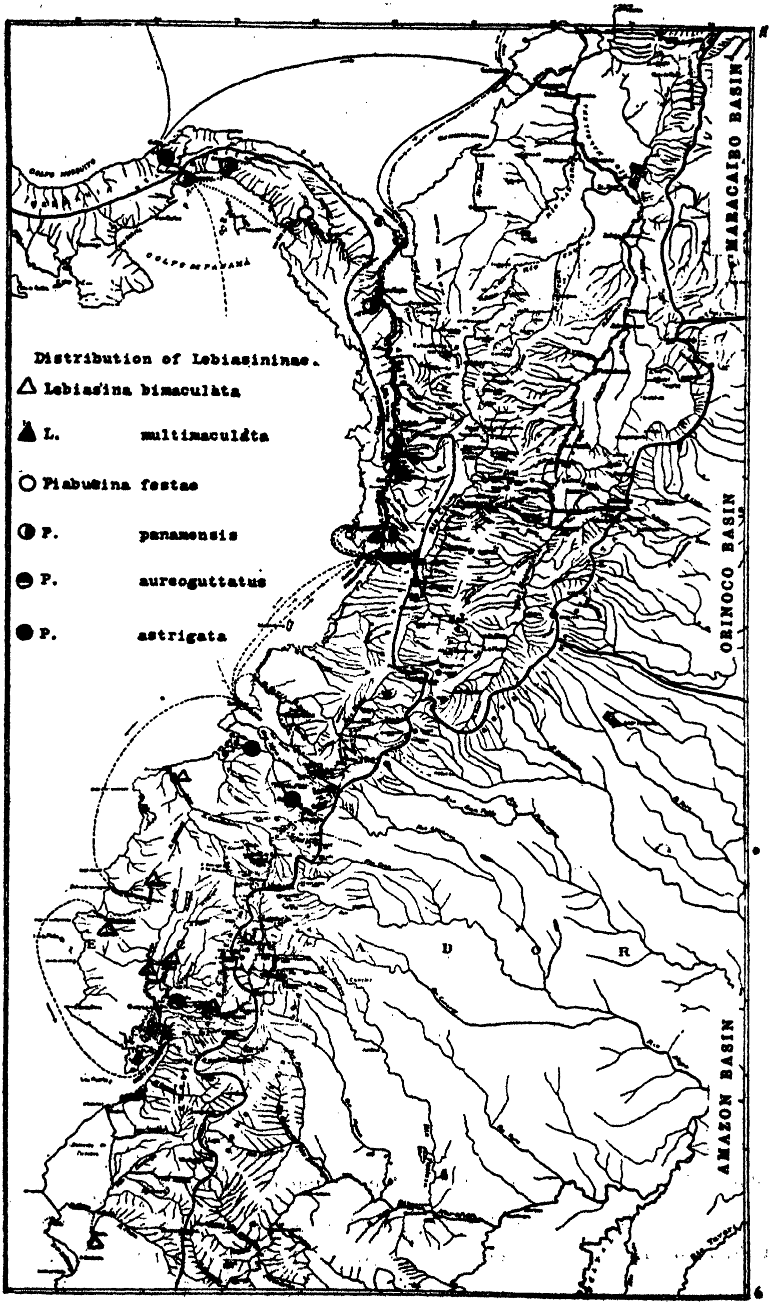

FIG. 4. The recorded localities in Ecuador and Colombia of the Huaicha and its relatives. The Huaicha itself extends south at least to central Peru.

I have taken it from sea level to over 7,000 feet, extending over more than the entire vertical range of yellow fever. Horizontally it occurs in all favorable places on the Pacific side between central Peru and central Ecuador. Related species are found between Guayaquil and Panama and species of a related genus are found on the Atlantic slope. In the restaurants at Lima this species is used as an ornamental aquarium fish. Its drawback is its tendency to jump out of the containers.

3. The Chalacos. This is a fish reaching over a foot in length and is found in tide pools and near the mouths of rivers from north Central Peru to California (Fig. 5). It has a "double" along the West Indian-Atlantic shores, and naturalists have veered from the opinion that the fishes on the two sides of Panama are identical to the notion that they are different. Certainly they are divergent forms of the same thing and the young of both sides ought to be available in mosquito work. Small specimens are said to do the work well, but do not survive the conditions as well as Lebiasina or Pygidium.

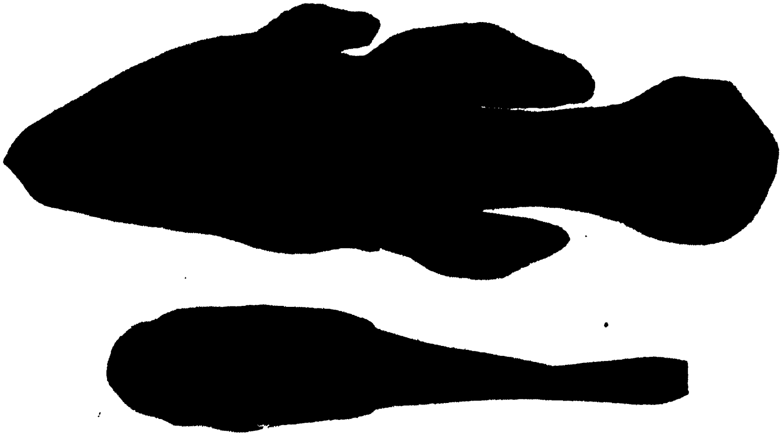

FIG. 5. The "Chalacos" of the coast.

I have caught Pygidium near the coast in Northern Peru. As far as known in Ecuador, they only occur at considerable elevations. In Guayaquil Huaijas and Chalacos are so cheap that it may not pay to use Pygidium.

# SYMBIOSIS IN ANIMALS AND PLANTS[1]

GEORGE H. F. NUTTALL, Sc.D., F.R.S.
THE UNIVERSITY OF CAMBRIDGE

## INTRODUCTION

THE subject of symbiosis has been chosen for this address because of its broad biological interest, an interest that appeals equally to the physiologist, pathologist and parasitologist. It is, moreover, a subject upon which much work has been done of recent years in different countries, and this seems a fitting occasion upon which to give a brief summary of what is known to-day, especially since the literature relating to symbiosis is largely foreign, somewhat scattered and relatively inaccessible.

## I. SYMBIOSIS IN PLANTS

### (1) *Lichens*

It is well known to botanists that the vegetative body (thallus) of lichen plants consists of two distinct organisms, a fungus and an alga. The alga, individual elements of which are called "gonidia," is either scattered throughout the thallus or, as in most cases, it forms a well-defined layer beneath the surface of the thallus. The view that lichens consist of the two elements mentioned was advanced by Schwendener (1867–69), who regarded the fungus as living parasitically upon the alga, a view which gained support from the researches of Bornet (1872), Voronin (1872), Treube (1873), etc., and especially of Bonnier (1886–89), wherein synthetic cultures were obtained by bringing together (*a*) various algae obtained in the open and (*b*) fungus-spores isolated from cultures of fungi forming the one component of certain lichens.

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[1] Address of the president of the Section of Physiology of the British Association for the Advancement of Science, Liverpool, 1923.

Schwendener's view, that the fungi are parasitic on the algae in lichens, was contested by Reinke (1873) on the ground that a state of parasitism did not explain the long and apparently healthy life of the associated fungi and algae, a biological association for which the term *Consortium* was proposed by him, that of *Homobium* by Frank (1876), and that of *Symbiosis* by de Bary (1879), the latter term denoting *a condition of conjoint life that is more or less beneficial to the associated organisms or symbionts.*

Investigation has shown that the relation or balance between the associated organisms varies in different lichens. Thus in some forms of *Collemaceae,* as stated by Bornet (1873), the partners as a rule inflict no injury upon each other, whilst in some species of *Collema* occasional parasitism of the fungus upon the alga (*Nostoc*) is observable, since short hyphal branches fix themselves to the alga cells, these swelling, their protoplasm becoming granular and finally being voided. In *Synalissa* and some other lichens the hypha penetrates into the interior of the alga, where it swells and forms a sucker, or haustorium. Elenkin (1902–06) and Danilov (1910) take it as proved that lichens owe their origin to parasitism, the fungus either preying upon the alga or living as an "endosaprophyte" (Elenkin) upon the algae that die.

Therefore, we may find in lichens the condition of true symbiosis on the one hand, ranging to demonstrable parasitism on the other, and, conversely to what has been described above, instances are known wherein algae are parasitic on fungi (Beijerinck, 1890).

## *Physiology of Lichens*

*The nutrition of algae in lichens* is similar to that of other chlorophyllaceous plants, the most important work on the subject being that associated with the names of Beijerinck (1890) and Artari (1902). In respect to nitrogen supply, Beijerinck cultivated various green algae, as well as gonidia derived from *Physcia parietina.* The gonidia only multiplied rapidly in a malt-extract culture-medium to which peptones and sugar were added. This showed that the algae associated with fungi as in lichens were placed advantageously in respect to nitrogen supply. He termed such fungi "ammonia-sugar-fungi," because they extract nitrogen from ammonia salts and, in addition to sugar, form peptones. Artari showed that there exist two physiological races in green algae, those which absorb and those which do not absorb peptones. He found that the gonidia (*Cystococcus humicola*) derived from *Physcia parietina* absorbed peptones, and he consequently referred to such algae as "peptone-algae." Treboux (1912), however, denies the existence of peptone-sugar-races of algae, and regards the algae in lichens as the victims of parasitic fungi. Nevertheless, the important researches of Chodat (1913) have demonstrated that cultivated gonidia develop four times as well when supplied with glycocoll or peptone in place of potassium nitrate.

The carbon supply of gonidia, according to Artari (1899, 1901), Radais (1900) and Dufrenoy (1918), is not derived photosynthetically, but from the substratum on which they grow. Whilst Tobler (1911), in his culture experiments with lichens, found that the gonidia obtain their carbon from calcium oxalate secreted by the fungus, Chodat (1913) observed that cultured gonidia grow but slowly without sugar (glucose), which he believes constitutes their main source of carbon supply.

Whereas, according to Chodat, the gonidia grow poorly on organic nitrogen in the absence of sugar, they develop rapidly when sugar is added. He therefore concludes that the gonidia lead a more or less saprophytic life in that they obtain from the fungus-hyphae both organic nitrogen and carbon in the form of glucose or galactose.

*The nutrition of fungi in lichens* depends partly upon parasitism, when they invade the gonidia, and partly upon saprophytism, when they utilize dead gonidia (Chodat).

In concluding this section, the hypothesis of M. and

Mme. Moreau (1921) demands mention, since it bears upon the manner in which lichens may have originated in nature. They regard the fungal portion as a gall-structure arising from the action of the associated alga. The lichen, according to this view, is to be regarded as a fungus that has been attacked by a chronic disease which has become generalized and necessary for the subsistence of the host-fungus. F. Moreau (1922) sums up this view as follows: "The lichen-fungus appears as an organism characterized in its morphology by deformity due to an infective agent, an alga. The history of the association existing in lichens may be described as that of a contagious malady marked by the invasion, development, inhibition, and death of the infective agent on the one hand, and on the other hand by the morphological reactions and defensive processes of the attacked organism. In conformity with the virulence and relative immunity of the two opponents, the struggle may be short, the association transitory, the conflict may last indefinitely and the association, rendered lasting, presents the appearance of a harmonious symbiosis."

### (2) *The Root-nodules of Leguminous and other Plants*

A well-known example of symbiosis is afforded by the presence of the bacteroids in the nodules of leguminosae, the micro-organisms being capable of fixing atmospheric nitrogen and thereby rendering nitrogen available for assimilation by the plant. This was demonstrated by Hellriegel and Willfahrt (1888), Schloesing and Laurent, whilst Beijerinck cultivated *Bacterium radicicola* from the nodules and produced nodules synthetically by bringing the plant and bacterium together on previously sterilized soil. According to Pinoy (1913), the bacteroids are myxobacteria, and, in the case of one species which he has especially studied (*Chondromyces crocatus*), it was found essential for the successful cultivation of the micro-organism, apart from its host-plant and in vitro, that it should be grown in association with a species of micrococcus; similar observations have been made on other micro-organisms by bacteriologists, and some refer to the conditions as one of symbiosis. Bacteriologists, I would note, are continuously misapplying the term symbiosis in referring to bacteria grown in mixed cultures, when there is no evidence whatever that the micro-organisms are mutually interdependent for their growth. In passing, it may be mentioned that nodules on the roots of the alder are attributed to the presence therein of *Streptothrices,* and that comparable nodules occur in Eleagnaceae. The nodules on the leaves of Rubiaceae and tropical Myrsinaceae are also regarded as due to bacterial symbionts.

### (3) *The significance of Mycorhiza in relation to various Plants*

It has long been known that the roots of *most perennial and arborescent plants* are invaded by the mycelium of fungi known as *Mycorhiza,* and it is to Kamiensky (1881), and especially Frank (1885), to whom we owe the hypothesis that we are here dealing with symbiotic life. Frank distinguishes two forms of *Mycorhiza*: (1) the *ectotrophic,* which surround the root externally like a sleeve and are found especially about the roots of forest trees (Conifers), and (2) *endotrophic,* which penetrate deeply into the root tissue and even into the cells of the root. The *endotrophic Mycorhiza* are derived from the outside; their mycelium enters the root by penetrating the epidermal cells at the base of the root hairs, passes between the cells and into them where the mycelium branches dichotomously, and forms ultimately a much-branched intracellular growth. By this time the fungus is no longer in communication with the exterior of the root, and it nourishes itself within the host cell, only, however, by utilizing the reserve substances stored there whilst avoiding the cell protoplasm or other living host elements. The host cell, after a period of inertia, exhibits a distinct reaction to the presence of the fungus, in that its nucleus becomes hypertrophied, divides repeatedly and becomes amoebiform in contour. The contained mycelial mass undergoes degeneration, is digested by the host, and the host-cell resumes its normal life. These root-*Mycorhiza* have not as yet been cultivated,[2] as have others to which reference will presently be made, and it is as yet impossible to assign them a place among known species of fungi. Further details regarding these forms will be found in the publication of Gallaud (1904).

### *Mycorhiza in Orchids*

The first to note the presence and to attempt to cultivate the fungus mycelium in the roots of orchids was Reisseck (1846), and in 1881 Kamienski advanced the hypothesis that the association was one of symbiosis. Wahrlich (1889) subsequently found symbionts in all species of orchids he examined, about 500 in number, thereby showing that their distribution is generalized.

It is to the researches of Noël Bernard (1902 onward), however, that we are actually indebted for the complete demonstration of the true relation existing between orchids and *Mycorhiza,* based as it is upon physiological studies. All who had to do with orchids in the last century found the greatest difficulty in raising these plants from their seed; a successful result appeared to depend largely on chance. Cultivators of orchids found that success was obtained more frequently by placing seed in soil upon which orchids had previously lived, and much secrecy was observed as to the methods employed by the more successful cultivators.

The seeds of orchids are exceedingly small—a million may be found in a single capsule of an exotic species; they possess no albumen and contain an embryo consisting merely of a mass of undifferentiated cells provided with a suspensor. The essential discovery of Bernard was that orchid seeds do not germinate in the absence of fungi belonging to the genus *Rhizoctonia.* The fungus enters the seed through its least resistant and highly permeable cells, which apparently emit a secretion that attracts the fungus. Each species of orchid, according to the subsequent researches of Burgeff (1909), possesses a special species, variety or race of fungus that is particularly adapted to it—he distinguishes fifteen species of fungus. When mutually adapted orchid seed and fungus are brought together, the mycelium of the latter penetrates the suspensor cells by digesting their cellulose wall. The mycelium traverses the epidermal cells of the seed without undergoing development within them. As soon as the primary infestation has occurred, even where the mycelium has penetrated but slightly, the cells of the seed, situated at the posterior pole of each embryo, cease to be vulnerable. In other words, a local immunity appears to be established, this immunity lasting at any rate until new regions are attacked by the fungus. This, in Bernard's experience, is the general rule. The mycelium, having attained the parenchyma cells, develops into characteristic filamentous masses recalling the appearance seen in bacterial agglutination. Nevertheless, there comes a time, this varying according to the associated species involved, when the development of the fungus is arrested by the deeper parenchyma cells of the seeds. These cells are altered before they are penetrated by the fungus; they become hypertrophied and acquire large lobose nuclei. They digest the mycelium which enters their protoplasm, but the cell continues to harbor remains of the fungus ("corps de dégénérescence") which occur abundantly in the tissues of orchids. The seed now proceeds to sprout, giving rise to a small tubercle ("protocorm"), which only at a later period produces leaves and roots.

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[2] Magrou (1921) reports that he isolated *Mucor solanum* n. sp. from *Solanum dulca-mara,* and he seems to have infected the potato plant with the fungus.

*The cultivation of Rhizoctonia* of various species was carried out successfully by Bernard, the cultures being used to reproduce germination in orchids. Orchid seeds alone remained unchanged for months in cultures on agar with salop-decoction added, but when pure cultures of

*Rhizoctonia* mycelium were added to such orchid seeds, the latter were invaded by the fungus, germinated, and gave rise to a "protocorm." Bernard gives excellent figures illustrative of the development described.

The relation between the fungi and orchids varies in different groups and plants. In primitive forms like *Bletilla* germination occurs in the absence of the fungus, but the "protocorm" does not develop; the rhizome, to which the plant is periodically reduced, is only periodically attacked when fresh roots are formed. *Bletilla,* however, behaves in an exceptional manner. In other orchids (*Ophrydeae, Cattleyeae, Cypripedeae,* etc.) the fungus is needed for germination, and the adult plant is fungus-free except when the orchid produces fresh roots. Therefore, in such cases symbiosis is intermittent. In higher orchids like the epiphytic *Sarcanthineae* the fungus is needed for germination, and, the roots being persistent, symbiosis is maintained continuously. Finally, in *Neottia nidus-avis* the symbiotic condition is maintained throughout the life-cycle of the orchid, the fungus being found in the roots, rhizome, and even in the flowers and seeds, and it is transmitted hereditarily.

*The activity or "virulence" of Rhizoctonia,* according to Bernard, diminishes when the fungus is kept apart from the orchid, being practically lost after two or three years. An attenuated fungus regains its activity in a measure after a sojourn of some weeks in a young orchid plant; a full degree of activity under symbiotic conditions is, however, only regained slowly.

*The germination of orchids in the absence of fungi* was successfully induced by Bernard through cultivating them in concentrated nutrient solutions of a kind that does not occur in nature; such solutions, moreover, except under carefully carried out experimental conditions, would be rapidly vitiated through serving as a medium for the multiplication of different micro-organisms. The effect of increasing the concentration of the solution, offered to plants reared without fungi, corresponds to that obtained by raising plants with fungi of increasing activity or "virulence." It may be added here that when *Rhizoctonia* are cultivated on a medium containing saccharose and the substance of orchid tubers—namely, salop—they cause an increase in the molecular concentration of the medium. It is possible that the fungi, when associated with the orchids, bring about a similar increase in the molecular concentration of the sap of the invaded plant.

### *The Origin of Tubers in Various Plants*

The occurrence of endotrophic *Mycorhiza* in the roots of species of *Solanum* has been recorded by Janse (1897) for *S. verbascifolium* in Java, by Bernard (1909–11) for *S. dulca-mara,* by Mme. Bernard and Magrou (1911) for *S. maglia* collected in Chili, the last-named species having been regarded by Darwin as the wild type of *S. tuberosum,* our edible potato.

Experimenting with the potato, Molliard (1907, 1920) found that tubers were not formed in aseptic cultures in a poor nutrient medium, and that raising the concentration of the sugar in the sap artificially (as with the radish) led to tuberization; concentrating the culture-medium did not induce tubers. Magrou (1921) placed potato seeds in a poor soil and close to *S. dulca-mara,* which always contains fungi, and found that only when the fungus invaded the potato plant were tubers formed.

Magrou also investigated tuberization in *Orobus tuberosus* (Leguminosae) and in *Mercurialis perennis* (Euphorbiaceae), and from his collective studies the following conclusions may be drawn:—

(1) When the potato plant and *Orobus* are raised from seed, the establishment of symbiosis leads to tuberization of the sprouts at the base of the stem; tubers are not formed in the absence of symbionts. (2) Owing to developmental differences between the two plants, symbiosis in the potato plant is intermittent, whilst in *Orobus* it is continuous. (3) It follows that these plants may develop in two ways: (*a*) when they harbor symbionts they

produce perennial organs; (*b*) without symbionts they are devoid of perennial organs. (4) It is the rule for wild perennials to harbor symbionts, as Bernard has stated, whilst annuals are devoid of symbionts; three species of annuals (*Solanum nigrum, Orobus coecineus* and *Mercurialis annua*) may be penetrated by endophytes, but they quickly digest the intruders. (5) These observations confirm and supplement the view held by Bernard that tuberization is due to the association of fungi with plants.

### *Mycorhiza in Ericaceae*

Rayner (1915–16) finds that *Mycorhiza* are constantly present in heathers. He isolated *Mycorhiza* (of the genus *Phoma*) from *Calluna vulgaris,* in which the fungus is widely distributed, being found in the roots, branches and even in the carpels, so that it occurs within the ripe fruit and seed tegument. *Calluna* seeds, when grown aseptically, give rise to poor little plants devoid of roots, but, under like conditions, in contact with *Phoma* the plants develop normally and form many roots.

### *Mycorhiza in Club-mosses and Ferns*

In Lycopodiaceae (Club-mosses) and Ophioglossaceae (Ferns), according to Bernard, the perennial prothallus is infested, and the spores whence the plants emanate will not germinate except (as with orchid seeds) with the help of fungi.

In concluding this part of my subject, dealing with symbionts of plants, I need scarcely emphasize the significance of symbiosis in the vegetable kingdom. I will close by mentioning the theoretical deduction of Bernard that vascular plants owe their origin in the past to the adaptation of certain mosses to symbiotic life with fungi.

## II. SYMBIOSIS IN ANIMALS

### (1) *Algae as Symbionts*

Animals of widely separated groups characterized by their green color have long been known. Already in

1849, von Siebold attributed the color of *Hydra viridis* to chlorophyll which, for a period, was regarded as an animal product. In 1876, Gésa Entz concluded that the chlorophyll is contained in vegetable cells living as parasites or commensals within the animals; these cells were aptly named *zoochlorella* by Brandt (1881), whilst cells distinguished by their yellow color were subsequently called *zooxanthella,* the latter having been first described by Cienkovsky (1871) as present in Radiolaria. In the latter case the symbionts were found capable of surviving their host, of multiplying and of assuming a flagellate stage.

Zoochlorella occur mainly in fresh-water animals, zooxanthella mainly in marine animals, the symbionts, measuring 3–10 microns in size, being found in many Protozoa, Sponges, Coelenterates, Ctenophores, Turbellaria, Rotifers, Bryozoa, Annelids and Molluscs.

*Physiological relations between Animals and Symbiotic Algae.*—In 1879, Geddes showed that green animals give off oxygen, *Convoluta roscoffensis* (Turbellaria), when well illuminated, liberating gas containing 45–55 per cent. of oxygen. Engelmann (1881), by means of his bacteria-method, showed that *Hydra viridis* (Coelenterata) and *Paramaecium bursaria* (Protozoa) give off oxygen when exposed to light. Geddes (1882), working with a series of marine animals, found *Velella* gave off 21–24 per cent. of oxygen, and an Actinia (*Anthoa cereus*) gave off 32–38 per cent. of oxygen. Whereas animals harboring green algae as symbionts always liberated oxygen, the colorless varieties of these animals never did so. Geddes regarded the association of animal and alga as being mutually helpful, the oxygen supplied by the alga to the animal and the carbon dioxide and nitrogen supplied by the animal to the alga being useful to the partners. He speaks of "animal lichens" and "Agricultural Radiolarians and Coelenterates." He found, moreover, that animals harboring symbionts are much more resistant than those without symbionts:

Medusae (*Velella*) survived 14 days in small beakers with symbionts, only 1–2 days without them. Protozoologists have, moreover, found that Protists harboring symbionts are easier to rear in vessels than are those without symbionts. Brandt (1883) believes that the symbionts and host aid each other in nutrition. Green *Spongilla* (fresh-water sponges) and *Hydra viridis* may live a long time in filtered water. He found that when starved green Actinia were (*a*) placed in the dark, they expelled their algae and died rapidly, being probably poisoned by the dead algae, but that when they were (*b*) placed in diffuse light they lived on. Actinia deprived of symbionts may become habituated in culture to live without them. Opinions (*vide* Buchner, 1921) are in conflict as to the exact relationship between the partners; in some cases (*Peneroplis* and *Trichosphaerium*) the symbionts never appear to be injured, in *Amoeba viridis,* etc., a limited number of symbionts are digested at all times, whereas in some Radiolarians, etc., digestion only takes place at certain stages of their development. Nutritive substances pass from the algae into the host's cells; thus starch granules, found alongside the algae, may be taken up by the animal cells.

Using modern methods of gas analysis, Trendelenburg (1909) concludes that green Actinias (*Anemonia sulcata*) live in true symbiosis with algae, the algae supply oxygen to the animal by day and at night utilize the surplus oxygen evolved, whilst carbon dioxide is furnished to the alga partly by the animal and partly by the water in which they are bathed. Rütter (1911) studied the nitrogen metabolism and concludes (*a*) that the Actinia yields to the algae nitrogen in the form of ammonia for protein synthesis, and in darkness it adds carbon containing substances (nitrogen-free), whilst (*b*) the algae yield to the Actinia nitrogenous substances in the dark and by light carbon-containing substances. Organisms harboring algae exhibit naturally a positive heliotropism.

Symbiotic algae are not usually transmitted hereditarily, each host-generation being usually infected afresh by algae, encountered about the host, which may be either free-living or possess a free-living stage in their development. Exceptions occur, however, where Protozoa multiply by division and the algae pass directly (as it were hereditarily) to succeeding generations. There are also cases of hereditary transmission in hosts that undergo sexual multiplication (as in *Hydra viridis*), the zoochlorella penetrating the egg on escaping from the host's endodermal cells after the manner of starch granules or other food reserve substances (v. *supra*). From the circumstances that in most cases symbiotic algae are not transmitted hereditarily, we may explain the occasional occurrence of alga-free individuals in a species usually harboring the symbionts.

Studies conducted on Turbellaria are of special interest: These animals may contain either green or yellow symbionts, and, as in Protozoa, some allied species harbor the symbionts and others do not. The eggs of Turbellaria are symbiont-free, each generation becoming infected afresh, the symbiont either entering the host's mouth and remaining there, traversing the intestinal wall, or entering by the genital pore, according to the particular host-species it affects.

The best-known example of symbiosis in Turbellaria is found in *Convoluta roscoffensis*, a species that has been well studied by Keeble and Gamble (1903–07). Its larvae are colorless and infection occurs after hatching. Colorless larvae are obtainable by transferring freshly hatched examples immediately to filtered sea-water. The cocoon, on the day following its deposition, is already invaded by many algae having a very different structure from those found in *Convoluta*; they possess four flagella and have been referred by Keeble and Gamble to the genus *Carteria* (allied to *Chlamydomonas*). The algae within the host possess a special structure, their contour is very irregular, they have no cellulose wall, the green coloring matter is unevenly distributed, being confined to chromatophore bodies surrounding the pyrenoid body, the nucleus is eccentric, and a number of examples are found with degenerating nuclei. Naturally all attempts to cultivate these obviously degenerating algae have failed.

The physiological relations existing between Turbellaria and algae differ according to the species. Thus in *Vortex viridis* symbiosis is not necessary, in *Convoluta* it is necessary for both partners. Mature *Convoluta* are never found devoid of algae in nature. The young larva can only feed itself for a week; as it grows older it becomes infected progressively with algae and ceases to nourish itself otherwise than upon the products of its contained symbionts. Finally, having reached an advanced age, the animal becomes capable of digesting the algae, as does *Convoluta paradoxa* under unfavorable conditions of life. Keeble and Gamble define four periods in the life of *Convoluta,* which they term respectively hetero-, mixo-, holo-, and auto-trophic, wherein the animal lives at the expense (1) of formed substances, (2) of these and alga-products, (3) of alga-products only, and finally (4) of the algae themselves. This constitutes a true evolution in a species from a free existence, depending only on outside sources of food supply, to a symbiontic mode of life, and lastly one merging into parasitism.

### (2) *Symbiosis in Insects*

Among insects we find a whole series of progressive adaptations toward an association with micro-organisms of different categories:

Group I.—*The utilization by insects of micro-organisms cultivated by them outside their bodies.* To quote three examples: (1) The larvae of the beetle *Xyloteres lineatus* (Bostrichidae) form galleries in the wood of Pines. The galleries have a characteristic blue color, produced by the growth of the fungus *Ambrosia* upon their walls, the fungus being cultivated by the larva for food. The beetle is incapable of digesting cellulose. Analogous cases occur among Ants and Termites thus:

(2) *Termes perrieri* of Madagascar, studied by Jumelle and Perrier de la Bâthie (cited by Portier, 1918), builds numerous chambers and galleries. The termites collect dead wood, chew it up finely, swallow it, the wood passing unaffected through their intestine and out in the form of small spherical masses (0.5 mm) which are cemented together as porous cakes that are impregnated with digestive secretions. Fungi which develop upon the cakes serve as food for the termites, and in well-cared-for nests the growth is harvested by the workers who triturate the mycelium and spores and feed the young larvae therewith, whilst older larvae receive spores, and large larvae receive mycelium and the triturated wood contained in the cakes. (3) A third example is that of ants belonging to the genus *Atta* which cultivate fungi over areas of 5 to 6 square meters; here the queen, when about to found a new colony, carries away a small ball of fungus in a corner of her mouth wherewith to start a fresh culture in the new habitat.

Group II.—*Symbiotic organisms developing in the lumen of the intestine and its adnexa.* As examples may be cited the bacteria occurring in the intestines of fly larvae (*Musca, Calliphora,* etc.), which aid the larva to digest meat; the bacteria associated with the olive-fly (*Dacus olea*); the Trychonymphids of xylophagous Termites (*Leucotermes lucifugus*).

Group III.—*Intestinal symbionts situated in the epithelial cells of the digestive apparatus.* The most striking instance is found in *Anobium paniceum,* a small beetle commonly occurring in flour, biscuits, dried vegetables, etc. In a part of its mid-gut are found cells filled with symbiotic yeasts undergoing multiplication (Escherich, 1900). The symbionts are not transmitted hereditarily but are acquired by the larva on hatching, being eliminated by the female beetle.

In this connection may be mentioned with reserve the observation of Portier (1918) upon xylophagous Lepidoptera (*Cossus, Nonagria, Sesia,* etc.) which, according to that author, possess intestinal fungi (*Isaria*) that multiply in the gut and form spores that penetrate the intestinal epithelium and attain the perivisceral cavity, fatbody and muscles of the insect. As Caullery points out, however, the supposed spores closely resemble Microsporidia, and Portier's interpretation may be erroneous. In this category also belong the symbionts described as occurring in *Glossina* by Roubaud (1919) and before him by Stuhlmann, these being found in certain hypertrophied cells of the intestinal epithelium. When liberated into the gut lumen, the symbionts are stated to multiply by budding after the manner of yeasts. Roubaud regards the yeasts as fungi, allied to the *Cicadomyces* of Šulç, and finds that they are transmitted hereditarily from the adult to the egg, larva and pupa.

Group IV.—*Intracellular symbionts of deep tissues.* This group of symbionts is most frequently found in insects, but their nature was not disclosed until recent years. Already, in 1858, Huxley described an organ which is constantly present close to the ovary in *Aphis*. Balbiani (1866) named it the pseudovitellus, or green body, and Metchnikoff (1866), who followed its development, named it "secondary vitellus." The function and structure of this organ were studied by subsequent authors without being understood until, in 1910, there appeared two important papers by Pierantoni (February 6), and Šulç (February 11), who demonstrated their symbiotic character, recognizing the intracellular inclusions as yeasts whose evolution they completely followed. Their results have been confirmed by various authors, especially by Buchner, who in a remarkable series of papers describes a number of associations existing between insects and micro-organisms and reaches important generalizations as to their significance. It is from a collective work on the subject by Buchner (1921) that most of our information regarding this class of symbionts is taken.

Among the symbionts of deep tissues in insects are found a whole series of specializations among the host-elements harboring the symbionts. The least specialized instance is represented by Lecaniinae where the yeasts are distributed throughout the body (perivisceral fluid, cells of fat-body); the fat-body cells may be regarded here as facultative Mycetocytes. In cases like *Orthezia,* symbiotic bacteria occur in certain fat cells which still contain fat droplets; this condition is also found in certain Cicadas, the yeasts being contained in fat cells which continue to accumulate fat, glycogen and urates. Finally cases occur as in Blattids where symbiotic bacteria are found in special cells greatly resembling fat cells but already forming well differentiated Mycetocytes. This class is well represented in and about the digestive tract of Pediculidae (*Haematopinus*) and certain ants (*Camponotus*). Still more advanced in specialization are those cases in which the symbiont-containing cells (*Mycetocytes*) agglomerate to form true organs termed *Mycetomas,* organs that are surrounded by flattened epithelial cells, the component mycetocytes containing either yeasts or bacteria as symbionts; such cases are found in Aphids, Chermids and Aleurodids. Mycetomas may occur singly or in numbers according to the nature of the host; the epithelial covering of the organ varies in its cell structure and pigmentation and the organ may be plentifully supplied with tracheae whose finest branches penetrate into the interior of the mycetocytes. The relations between the mycetocytes or mycetomas and the other organs of the host vary greatly; in some cases they occur especially in the fatty tissue, in others near the gonads, in others, as in Pediculidae, around or upon the intestine. In *Pediculus* and *Phthirus,* parasitic on man, the mycetoma is disc-shaped and lies centrally as a distinct milk-white structure upon and indenting the mid-gut. Transition forms between isolated mycetocytes and differentiated mycetomas are found in various insects.

*The mode of transmission of intracellular symbionts of insects* from generation to generation may take place in different ways as defined by Buchner (1921, somewhat modified):

I. The larva of each generation infects itself through the mouth (Anobiidae).

II. Infection takes place hereditarily through the egg:

1. By symbionts set free in the blood, or which leave mycetocytes or mycetomas and attain the egg as follows:
    (*a*) by general infection of follicles and invasion of the egg, and finally establishing themselves at the posterior pole of the egg (Ants);
    (*b*) by penetrating special parts of the follicles, producing for a period bacterial vegetation upon the whole egg and finally concentrating at the egg's two poles (Blattidae);
    (*c*) by entering the egg *via* its nutritive cells
        (*a*) only some isolated fungi entering (Lecaniinae);
        (*b*) a number of bacteria enter in the form of a gelatinous mass (Coccinae);
    (*d*) by entering the posterior pole of the egg:
        (*a*) as isolated fungi
            (*a*) which penetrate one after another (Aphids);
            (*b*) which accumulate in follicles and enter in a mass consisting of
                (*a*) one kind of symbiont (Icerya);
                (*b*) two kinds of symbiont (Cicada, Aphrophora);
                (*c*) three kinds of symbiont (Aphalara ?);
        (*b*) as bacteria united in several gelatinous masses (Orthezia).
2. By whole mycetomas entering at posterior pole of egg (Aleurodes).
3. By isolated symbionts leaving special mycetomas situated at juncture of follicular tubes (Pediculidae).

III. Embryonal infection as in parthenogenetic Aphids.

It is difficult to understand the mechanism whereby the symbionts penetrate the egg in the insect's body; in any case the complicated procedure must depend upon a mutual and parallel adaptation of the insects and microorganisms concerned.

During embryonal development the topographical distribution of the mycetocytes varies from one group of insects to another. In *Camponotus* they occur dorsally upon the mid-gut; in Blattidae the bacteria are at first localized in the intestinal lumen, passing thence through the intestinal epithelium and entering the fat-cells. In Hemiptera and Pediculidae the symbionts form a mass at the posterior pole of the germinal layer, and during version or unrolling of the embryo they penetrate in the ventral region of the abdomen.

As already indicated, the symbionts may be Yeasts, Saccharomycetes, Bacteria, or even Nitrobacteria. Their entrance into the cells and their presence therein even in large numbers does not in many cases prevent multiplication of the invaded cells or affect their mitosis; in other cases mitosis is more or less affected; it may become multipolar and lead to synsytium formation; and finally, cases may occur in which mitosis ceases and the symbiont-bearing cells divide amitotically.

We know little regarding the part played by symbionts in insects; our information relates almost exclusively to their morphology, mode of multiplication, and entry into the host during its development. There are no indications that the symbionts are injurious or pathogenic. It is evident, however, that they find in certain insects favorable conditions for growth, multiplication and transmission from host to host. In these cases, therefore, we are dealing with a constant very harmonious association which excludes even a suspicion of there being any conflict between the associated organisms. We may well ask ourselves what are the reciprocal advantages of this association, but this is a question that it is impossible to answer in view of our ignorance of physiological and biochemical processes in insects.

Various hypotheses have been advanced to explain the possible function of the symbionts. Symbiotic yeasts may decompose urates (Šulç); they may produce an enzyme that aids in digestion of sugars, as in Aphids (Pierantoni); they may aid in digestion of cellulose in xylophagous insects which alone can not render cellulose assimilable (Portier); the Nitrobacteria found in various Hemiptera may fix free nitrogen which is conveyed to them through the host's tracheae, and thus supply the host with nitrogenous substances, thereby meeting a deficiency in its food supply.

Phytophagous Hemiptera nourish themselves chiefly upon leaf-sap without utilizing the protoplasm of the plant-cells they penetrate with their sucking mouthparts. The imbibed sap is rich in mineral substances, carbohydrates and glycosides only. In these insects Peklo finds two different symbionts, Saccharomycetes and coccoid organisms, whilst Pierantoni attributes to symbionts the pigment production in *Coccus cacti.*

### (3) *Micro-organisms in Relation to Luminescence in Animals*

A fairly large number of organisms are known which have the faculty of emitting light. They are found among Bacteria, Fungi, Protozoa, Coelenterates, Echinoderms, Worms, Molluscs, Crustacea, Insecta, Tunicata and Fish. As a rule luminescence in animals depends upon the action of luciferase on luciferin, but recently a number of cases have become known wherein light production has been traced to micro-organisms, and it is with these cases that we shall deal.

Luminescent pathogenic bacteria may invade the host, as described by Giard and Billet (1889–90), for the small marine amphipod, *Talitrus,* of which rare light-emitting examples may be found in nature. The affected crustacean dies in about six days. The pathogenic bacterium does not luminesce in cultures, but does so when inoculated into *Talitrus.*

Luminescent symbiotic bacteria present in various light-emitting animals are, however, of direct interest to us, since their presence has been determined in luminescent organs of certain insects, cephalopods, tunicates and fishes:

Insects: Pierantoni (1914) investigated the luminous organs of glow-worms (*Lampyrus*), and found them to consist of parenchyma cells crowded with minute bodies having bacteria-like staining reactions, these bodies being also present in the beetle's egg, which is luminous. He cultivated two species of micro-organisms from the organs, but does not distinctly establish their causal relationship.

CEPHALOPODS: We owe to Pierantoni (1917–20) and Buchner the discovery that luminescence in certain Cephalopods is due to light-producing bacterial symbionts living in special organs of the host. These organs may be simple or otherwise. In *Loligo* the luminous organs, hitherto known as "accessory nidamentary glands," represent the simpler type of organ, this consisting merely of a collection of epithelial tubes surrounded by connective tissue. In cuttle-fish (*Sepiola* and *Rondeletia*) the organs are more complicated, the glands being backed by a reflector, and provided outwardly with a lens serving for the projection of the light rays generated by the symbionts within the tubes. The symbionts are transmitted hereditarily when the Cephalopods lay their eggs. The symbionts of *Loligo* and *Sepiola* have been cultivated by Pierantoni and Zirpolo (1917–20); they inhabit the gland-tubes of the luminescent organs in large numbers, and produce light continuously, as do other luminescent bacteria in cultures.

TUNICATA; The Pyrosomidae, all of which emit light and form tubular colonies, have long attracted the attention of biologists. Each individual in the colony possesses two fairly large luminescent organs, whose structure was studied by Panceri (1871–77), Kovalevsky (1875), and especially Julin (1909–12), who observed in the cells of the luminous organ riband-like structures appearing knotted here and there. Julin regarded the structures as mitochondria or chromidia, and it was left to Buchner (1914) to explain their true nature; they are symbiotic fungi, and are transmitted hereditarily. Buchner gives a detailed study of the symbiont and a review of the physiology of luminescence and of Pyrosomes which is well worth consulting by those interested in such problems.

FISH: Of great interest are the researches of Harvey (1922) upon light production by two species of fish (*Photoblepharon* and *Anomalops*) which occur in the sea about the Banda Islands, Moluccas. Their life-history is unknown. They measure up to about 11 cm in length. The author writes: "In both fishes the luminous organ is a compact mass of white to cream-colored tissue, flattened oval in shape, lying in a depression just under the eye and in front of the gills. The organ looks as if made for experimentation, as it is attached only at the dorso-anterior end, and can be cut out with the greatest ease, giving a piece of practically pure luminous tissue. The back of the organ is covered with a layer of black pigment, which serves to keep the light from shining into the tissues of the fish. In both fishes there is a mechanism for obscuring the light, but, curiously enough, the mechanism developed is totally different in the two species, notwithstanding the fact that in structure the organ is identical in the two, and in every detail except proportion the fishes are very similar. In *Anomalops* the organ is hinged at the antero-dorsal edge, and can be turned downward until the light surface comes in contact with a fold of black pigmented tissue, forming a sort of pocket. The light is thus cut off. In *Photoblepharon* a fold of black tissue has been developed on the ventral edge of the organ socket, which can be drawn up over the light surface like an eyelid, thus extinguishing the light." The histological structure of this organ was worked out by Steche (1909). The organ is continuously luminous day and night, and independent of stimulation. According to Steche, *Anomalops* constantly turns the light on and off (10″ light, 5″ dark), the fish using it, he supposes, as a searchlight to attract and mislead its prey. The natives use the amputated organ as a bait in night fishing; it maintains its luminosity for about eight hours. The organ is described by Steche as composed of a great number of sets of parallel gland tubes (acinose), separated by connective tissue, and extending across the organ from the back pigmented surface to the front transparent surface, each set arranged in a ring about a vessel which provides them with blood and oxygen. Near the surface a number of these tubes unite into a common reservoir, opening outward through a minute pore which admits sea-water. A number of pores dot the surface of the organ. The luminous material fills the lumen of the tubes; it is extracellular but intraglandular, and is never voided from the gland. Harvey states that the luminous material filling the tubes consists of an emulsion containing many granules and rods; the latter move about with a corkscrew-like motion, and are undoubtedly bacteria. The luminosity of the organ is due to these symbiotic bacteria. An emulsion containing the symbionts behaves exactly like an emulsion of luminous bacteria in being sensitive to lack oxygen, desiccation, bacteriolytic agents, potassium cyanide, etc. The continuity of the light, independently of stimulation, is characteristic of luminous bacteria and fungi alone among organisms; this, and the circumstance that luciferin and luciferase could not be demonstrated, all go to confirm the correctness of Harvey's conclusions regarding the cause of luminosity in these fish, notwithstanding that he has failed hitherto to cultivate the bacteria found in the luminous organs.

In concluding this section dealing with light production by animals it may be repeated that we have to distinguish between (*a*) luminescence due to symbiotic organisms, such luminescence being continuous in the presence of oxygen as in cultures of luminous bacteria (of which some thirty species are known), and (*b*) that due to animal cell-products known as luciferin and luciferase which are secreted and expelled *at intervals,* in response to a stimulus, from two kinds of gland cells, the secretions, when mixed, producing light.

## *Portier's Hypothesis*

The numerous cases in which symbiosis occurs in nature have naturally led some biologists to ask if symbiosis is not a phenomenon of general significance, and perhaps essential, in living organisms. In this connection reference must be made to the hypothesis advanced by Portier (1918), because it formulates extreme views. Starting from his studies of symbionts of leaf-mining caterpillars (*Nepticula*) and wood-devouring insect larvae (*Cossus, Sesia,* etc.), he sought to verify the work of Galippe (1891–1918) on micro-organisms occurring in vertebrate tissues. Using methods he supposed to be adequate, Portier claimed that he could isolate various micro-organisms from vertebrate tissues. On faulty premises he built up a hypothesis that may be likened to a house of cards. He divides living organisms into two groups, *autotrophic* (bacteria only) and *heterotrophic* (all plants and animals), according as they are provided or not with symbionts. Whereas some symbionts are cultivatable, others have become so domesticated in respect to their hosts that they can not be separated from them. The essential function of symbionts is to elaborate reserve substances so that they become assimilable to the host cell. The mitochondria that are present in all plant and animal cells, though not cultivatable, are, according to Portier, nothing but symbionts, the importance of their function having recently been revealed by Guillermond, Dubreuil and others.[3] They are derived from food, and, if absent therefrom, illness supervenes, as shown by the bad effects of sterilized food, decorticated rice, etc., causing deficiency diseases attributed to lack of vitamines, which, according to Portier, are nothing but symbionts. Where, as in *Aphis,* the animal feeds on plant sap that is filtered through a tube formed by the insect's saliva—in other words, the insect imbibing food devoid of symbionts —the animal is of necessity provided with its own well-developed store of them. Portier applies his hypothesis to such varied problems as fecundation, parthenogenesis, tumor-formation, variation and origin of species, in all of which mitochondria, that is, his supposed symbionts, play a part. His views aroused great controversy in France, so much so that it was thought necessary for the Société de Biologie de Paris (see C. R. Soc. Biol., LXXXIII, 654,

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[3] Guillermond has shown that the mitochondria of the epidermal cells in *Iris* elaborates amyloplast and finally starch. Dubreuil (1913) found that mitochondria elaborate the fat in fat-cells. Other cytologists have shown that glandular secretions are similarly referable to mitochondria.

May 8, 1920) to have a Committee examine the evidence. The Committee, consisting on the one part of Portier and Bierry, and on the other of Martin and Marchoux (Institut Pasteur), by its report indicates the pitfalls, well known to bacteriologists, into which Portier was led, and thus disposes of the greater part of his far-reaching hypothesis. Nevertheless, like many exploded hypotheses, that of Portier has served a useful purpose through the discussion it has provoked and the interest in the subject of symbiosis which it has stimulated.

## CONCLUSION

The term "symbiosis" denotes a condition of conjoint life existing between different organisms that in a varying degree are benefited by the partnership. The term "symbiont," strictly speaking, applies equally to the partners; it has, however, come to be used also in a restricted sense as meaning the microscopic member or members of the partnership in contradistinction to the physically larger partners which are conveniently termed the "hosts" in conformity with parasitological usage.

The condition of life defined as symbiosis may be regarded as balancing between two extremes—complete immunity and deadly infective disease. A condition of perfect symbiosis or balance is realized with comparative rarity because of the many difficulties of its establishment in organisms that are either capable of living independently or are incapable of resisting the invasion of organisms imperfectly adapted to communal life. In these respects the conclusions of Bernard and Magrou in relation to plants apply equally to animals. It is difficult to imagine that symbiosis originated otherwise than through a preliminary stage of parasitism on the part of one or other of the associated organisms, the conflict between them in the course of time ending in mutual adaptation. It is, indeed, probable that some supposed symbionts may prove to be parasites on further investigation.

In perfect symbiosis the associated organisms are completely adapted to a life in common. In parasitism the degree of adaptation varies greatly; it may approach symbiotic conditions on the one hand, or range to vanishing point on the other by leading to the death of the organism that is invaded by a highly pathogenic animal or vegetable disease agent. There is no definite boundary between symbiosis and parasitism. The factors governing immunity from symbionts or parasites are essentially the same.

No final conclusions can as yet be reached regarding the function of symbionts in many invertebrate animals owing to our ignorance of the physiological processes in the associated organisms. The investigation of these problems is one fraught with difficulties which we must hope will be surmounted.

New knowledge is continually being acquired, and a glance into new and even recent publications shows that symbionts have been repeatedly seen and interpreted as mitochondria or chromidia. Thus in *Aphis* the long-known pseudovitellus has been shown to contain symbiotic yeasts by Pierantoni and Šulç, independently and almost simultaneously (1910); Buchner (1914) has demonstrated symbiotic luminescent fungi in the previously well-studied pyrosomes, besides identifying (1921) as bacterial symbionts the mitochondria found by Strindberg (1913) in his work on the embryology of ants. The increasing number of infective diseases of animals and plants, moreover, which have been traced, especially of recent years, to apparently ultramicroscopic organisms, can not but suggest that there may exist ultramicroscopic symbionts.

From the foregoing summary of what is known to-day of symbiosis we see that it is by no means so rare a phenomenon as was formerly supposed. Symbiosis occurs frequently among animals and plants, the symbionts (Algae, Fungi, Bacteria) becoming in some cases permanent intracellular inhabitants of their hosts, and at times being transmitted from host to host hereditarily. Among parasites, non-pathogenic and pathogenic, we know of cases wherein hereditary transmission occurs from host to host.

It is evident that we are on the threshold of further discoveries, and that a wide field of fruitful research is open to those who enter upon it. In closing, it seems but fitting to express the hope that British workers may take a more active part in the elucidation of the interesting biological problems that lie before us in the study of symbiosis and the allied subject of parasitism.

*Acknowledgment.*—I have pleasure in expressing my thanks to my colleague, Mr. David Keilin, for the very valuable aid he has given me in the preparation of this address.

# SHORTER ARTICLES AND DISCUSSION

## THE ABSENCE OF LUTEAR CELLS IN THE TESTIS OF THE MALE PHALAROPE

CERTAIN experiments that I carried out several years ago with sebright bantams, in which breed of fowls the plumage of the male is like that of the female, showed that the suppression of the cock-feathering of the male is due to some hormone produced by the testis. It is known that a hormone produced in the ovary of the female of other races of domestic fowls also inhibits the development of cock-feathering in the female. Whether this substance is the same as that produced in the testis of the male sebright has, however, not been shown.

In the testis of the male sebright certain cells are present that resemble the so-called lutear cells of the ovary of the female sebright, and of the ovary of females of ordinary fowls. These cells are absent, or rare, in the testis of adult males of ordinary breeds. I suggested, therefore, that the inhibiting hormone of the male sebright is produced by these cells. This hypothesis was, I believe, justified by the evidence, which could not, however, be claimed to be more than circumstantial.

The condition of the sebright is almost unique amongst birds. As a rule the male bird has a more highly developed plumage than the female. One of the rare exceptions to this rule is shown by the phalarope, in which the female is more highly colored than the male. An opportunity to examine the gonads of this bird arose when I was in California in 1920. In the autumn of that year I shot a few birds (*Lobipes lobatus*), adult and young, female and male, and made preparations of their ovaries and testes. In the ovaries the characteristic lutear cells were found, but none could be detected in the testes either of the juvenile or of the adult males. I delayed publishing the result (or lack of result) because I hoped to procure males in the spring, during their migration northward, but so far I have not been successful. However, it is improbable that the spring birds would be different from the autumn migrants with respect to the lutear cells. In a recent number of the *Anatomical Record* (xxiv., No. 6, 1923) Yocum reports, in fact, the absence of lutear cells in the testis of the phalarope both in the spring and in the autumn migrants.

The absence of the lutear cells in the testis of the male phalarope shows that his failure to develop a plumage as highly colored as that of the female can not be ascribed to such cells. Whether other cells in the testis of these birds produce a hormone that acts as an inhibitor can only be found out by castration. It is, of course, just as likely that the result may be produced in some other way or by other cells. The absence of lutear cells does not count either for or against the view that these cells are the agents in the male sebright that keep his plumage down to that of the female.

I think that too much emphasis is being placed on my hypothesis that the lutear cells in the sebright produce the hormone that suppresses the cock-feathering. It is a matter of secondary importance what cells in the testis of the male sebright produce the hormone. The important result is not the identification of these cells, but rather the demonstration through castration that something is produced by the testis of the male sebright that suppresses the full development of his plumage. This is the result that I should wish to emphasize rather than that the results are brought about by lutear cells. The latter view is hypothetical and, as I have said, is based only on circumstantial evidence. Nevertheless, I still think that the evidence makes this interpretation probable, and that it is not affected by the results here recorded for the phalarope.

T. H. Morgan

Columbia University

## THE VERTEBRAL FORMULA IN THE SAUROPODA

I have had occasion recently to very carefully study the excellent paper by Messrs. Osborn and Mook upon the osteology of *Camarasaurus*, etc., published with a profusion of figures and plates in the *Memoirs* of the American Museum of Natural History, Volume III, Part III. The paper deals with the material representing the Sauropoda collected for Professor E. D. Cope near Canyon City, Colorado, and now possessed by the American Museum of Natural History.

All students of the skeletal structure of the dinosauria have been placed under obligation by this monograph, the difficulty of preparing which can only be realized by the small coterie of those who have been called upon to make similar studies. Not only are many of the bones heavy and on that account difficult to handle, but in the case of Cope's material they have been more or less crushed and distorted. Unfortunately, as is pointed out by the authors, the original records, if there were any in the possession of Professor Cope, have been lost, and it is impossible at this late day to ascertain what were the exact relations of the different skeletal remains as they originally were found in the quarries.

There is one important point in which I find myself constrained to differ from the conclusions reached by the learned authors of this monograph. Osborn and Mook state on page 291 that "*Apatosaurus* is known to have thirteen cervicals, including the atlas and axis." Upon what this positive statement is founded is not made clear by the writers. It is, I think, open to question. The Carnegie Museum has in its possession a practically complete skeleton, which we have referred to the genus *Apatosaurus*, and this skeleton shows that the cervical vertebræ were *fifteen* in number, including the atlas and axis. Professor Hatcher ascertained beyond the possibility of question that in the genus *Diplodocus* there were fifteen cervical vertebræ, including the atlas and axis. I am strongly of the opinion that *Camarasaurus* possessed fifteen cervical vertebræ, as was the case in the other two genera, to which allusion has just been made, and in which the number of cervical vertebræ has been definitely ascertained. Furthermore, we have in our possession at the Carnegie Museum a cervical vertebra belonging to *Camarasaurus* obtained from one of the same quarries from which Cope's material was taken, and which appears to be a posterior cervical, differing from all of those figured by Osborn and Mook in certain particulars, and in such a way as to suggest that it is one of the posterior cervicals, which they did not possess at the time they were working up the material upon which they founded their memoir. Whether it is the fourteenth or the fifteenth it is hard to say, but it appears to be intermediate between the first dorsal, as figured by Osborn and Mook from more or less fragmentary material, and the last cervical which they have called the thirteenth.[1] In view of the positively ascertained fact that in the related genera *Apatosaurus* and *Diplodocus* there are fifteen cervicals and the fact that we possess a posterior cervical which was apparently unknown to Osborn and Mook, I am inclined to maintain, until convinced to the contrary, that *Camarasaurus* in all probability possessed fifteen cervical vertebræ.

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[1] There is probably another missing cervical in the holes which Prof. Cope caused to be made, and which may turn up at some future time when further explorations are made in these localities.

There is other material, representing other allied genera, which the writer is engaged at the present time in closely studying, as fast as it can be removed from the matrix, which goes to confirm the view which I have just expressed.

The number of vertebræ entering into the composition of the sacrum has been the subject of some diversity of opinion. I am inclined to think that the view expressed by others and accepted by Osborn and Mook that the vertebræ of the sacrum in the Sauropoda are five in number, of which three are primary, preceding which is the dorso-sacral, and succeeding which is the caudo-sacral, is correct. This view is confirmed by all the material at my command, consisting of numerous sacra of sauropods. Osborn and Mook point out very aptly that the degree of coossification between the dorso-sacral and the caudo-sacral and the three primaries varies with age. As a rule the caudo-sacral coossifies more completely with the three primaries and with the ilia than the dorso-sacral. In fact the caudo-sacral, even in young specimens, appears in the different genera to constitute an integral part of the sacrum. So far as is known to me there are very few sacra which have been collected in which the caudo-sacral is not firmly united with the antecedent primary series. It is doubtful whether the sacra in which the three primaries alone are found are in perfect condition. Such a sacrum with only three primaries was figured by Professor O. C. Marsh in the case of *Apatosaurus ajax* and *Atlantosaurus montanus* (*Cf. American Journal of Science,* Vol. XVII, 1897, pl. VI, figs. 1 and 2). My impression is that these sacra are both defective specimens, but the temporary inaccessibility of Marsh's material, owing to the fact that the Peabody Museum is undergoing reconstruction, prevents me at present from confirming this view. These sacra are either defective, or are the sacra of young and immature individuals.

The conclusion which I desire to advance in reference to the vertebral formula in the Sauropod dinosaurs is represented in the following formula, which is advanced as representing the latest generalization upon the subject, largely based upon the material in the possession of the Carnegie Institute.

Vertebral Formula in the Sauropoda

| | | | |
|---|---|---|---|
| Cervicals, including atlas and axis | | | 15 |
| Dorsals | | | 10 |
| Sacrals | Dorso-sacral | 1 | 5 |
| | Primary sacrals | 3 | |
| | Caudo-sacral | 1 | |
| Caudals according to genera | | | 32–82 |

It is, of course, possible, as more and more material is acquired and studied, that the foregoing formula may be found in one or the other genus of the Sauropoda to show variation in the number of the cervicals. The presumption, however, is strong that the various genera will be found in the end to have the same number of cervicals, dorsals and sacrals. The number of caudals is always likely to reveal more or less generic and even individual variation.

W. J. Holland

Carnegie Museum

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# TRISOMIC INHERITANCE IN THE POINSETTIA MUTANT OF DATURA

DR. ALBERT F. BLAKESLEE AND M. E. FARNHAM
STATION FOR EXPERIMENTAL EVOLUTION, COLD SPRING HARBOR, N. Y.

## INTRODUCTION

THE phenomenon of mutation in the jimson-weed (*Datura Stramonium*) has already been discussed in earlier publications (1–10), in which it has been shown that the presence of an extra chromosome exerts an unbalancing effect upon the make-up of the individual plant. That the extra chromosome is a member of a particular chromosomal set and exerts its influence in $(2n+1)$ mutants by virtue of the specific factors which it contains was first clearly indicated by unexpected color ratios obtained in breeding the mutant Poinsettia. Earlier publications (6, 3, 4) have given an outline of the evidence then available which had led to the conclusion that the Poinsettia mutant, as well as its variety Wiry, has its extra chromosome in the set carrying the factors for purple and white flower color. The present paper will give the results of a further and more detailed study of the inheritance of color in this mutant which amply justify, we believe, the conclusion reached from the earlier and less extensive data. Inasmuch as a belief in the specificity of the extra chromosomes associated with the various unbalanced mutant types has been the starting point for a series of investigations in Datura, the basis for this belief seems to warrant a thorough investigation. The reason Poinsettia was chosen for intensive study rather than the mutant Cocklebur, in which the extra chromosome apparently has been identified as a member of the set carrying the factors for armed and inermis capsules, is because plants can be classified for color characters at an early stage—in fact, as soon as the seedlings are above the ground—while plants must be grown to the fruiting stage before the type of capsule is discernible.

## DESCRIPTION OF POINSETTIAS

When grown in the field the adult Poinsettia is the most striking in appearance of all our mutants. Its long narrow dark-green leaves are clustered at the ends of branches in a fashion which was suggestive of the plant for which it has been named (5, Fig. 14). Towards the latter part of the growing season, masses of adventitious growth extrude in longitudinal lines from young stems, causing irregularities in the branching. Its internal anatomy (10) differs radically from the normal type. The capsule is nearly spherical, large and beset with long spines (4, Figs. 4 and 5). Frequently the floral parts are malformed by an increase in the number of stamens, lobes of calyx and corolla and divisions of the pistil. It is often difficult to induce the capsules to set on plants grown in the field, but less difficulty is experienced in obtaining seeds from plants grown in pots in the greenhouse.

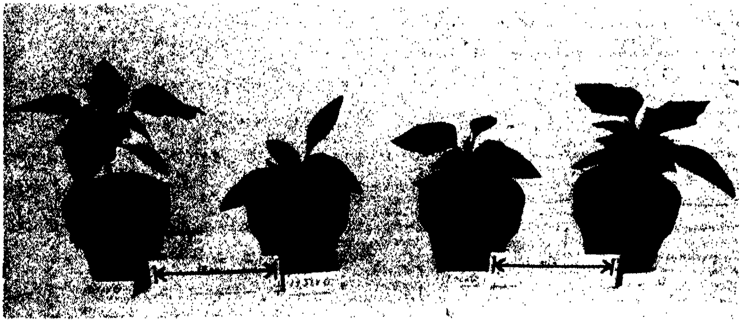

FIG. 1. Two seedling Poinsettias in center in 3-inch pots with normals from same fraternity on either side, photographed at stage before plants are recorded.

Pot-grown Poinsettias (Fig. 1) are not so distinct as field-grown plants, but can readily be distinguished by one familiar with their appearance. The leaves of seedlings are longer and narrower, have relatively fewer teeth and are slightly more depressed at the veins in comparison with normals. The majority of our Poinsettia cultures have been grown in the greenhouse and recorded from three-inch pots for reasons of economy. In all cases where doubt has arisen as to the classification of such seedlings, the plants in question have been grown to a stage when they could be recorded with certainty. We do not believe, therefore, that increased accuracy would have resulted from growing our Poinsettia cultures in the open where the numbers that could have been conveniently handled would have been greatly diminished.

## INHERITANCE OF POINSETTIA COMPLEX

The inheritance of the Poinsettia complex resolves itself into the transmission, through the male and female gametes, of the extra chromosome which brings about the peculiarities of this $(2n+1)$ mutant. If the $(n+1)$ gametes functioned equally with the $n$ gametes and the $(2n+1)$ zygotes had the same survival value as the $2n$ zygotes, we should expect from selfing Poinsettias the following offspring: $1(2n+2\mathrm{P}n)+2(2n+1\mathrm{P}n)+1(2n)$, and from crossing Poinsettias with normals we should expect $1(2n+1)+1(2n)$. That the numbers of $2n$ and of $(2n+1)$ offspring from the latter combination are not equal in Table I is apparently due in Poinsettia as in Globe (2) to the unbalancing effect exercised by the extra chromosome upon the female gamete and the zygote. The decrease in vigor thus affected is perhaps somewhat less severe in Poinsettia than in Globe. The unbalancing effect is naturally greater in the gametes (1 vs $n$) than in the zygote (1 vs $2n$) and apparently causes an abortion of the pollen grains (3, Table I) or a retardation of the growth of the pollen tubes (9) affected. The result is that few if any pollen grains transmit the Poinsettia complex. This fact would tend to prevent the appearance of $(2n+2)$ Poinsettias which, judging from the $(2n+2)$ Globes, might be expected to have a low survival value.

TABLE I

INHERITANCE OF POINSETTIA COMPLEX WITHIN LINES 1 AND 2

| | Poinsettia<br>Selfed | Poinsettia<br>×<br>Poinsettia | Poinsettia<br>×<br>Normal | Normal<br>×<br>Poinsettia |
|---|---|---|---|---|
| Number of Seed Parents | 75 | 32 | 41 | 2 |
| Normals | 5316 | 3041 | 2864 | 1126 |
| Poinsettias | 2098 | 1384 | 1304 | 0 |
| Per cent. Poinsettias | 28.30 ± .353 | 31.28 ± .470 | 31.29 ± .484 | 0.00 |

Percentage difference between offspring from Poinsettia selfed and from Poinsettia × Normal = 2.99 ± .599. Diff./P.E. Diff. = 4.99.

Difference between offspring from Poinsettia selfed and from Poinsettia × Poinsettia = 2.98 ± .588. Diff./P.E. Diff. = 5.07.

The extra chromosome is transmitted to slightly fewer offspring when a Poinsettia is selfed than when it is crossed with a normal or with another Poinsettia as pollen parent. The difference is not great but seems to be significant statistically. A similar but greater difference was found in Globe crosses (2) and may most reasonably be attributed to a difference in vigor of zygotes obtained respectively from selfing and from crossing. In the Globe crosses several diverse lines were involved, while in the Poinsettia crosses shown in the table only two closely similar lines (Lines 1 and 2) are represented.

## OCCURRENCE OF NEW POINSETTIAS

Poinsettia is not an uncommon form among our $(2n+1)$ mutants. In Table II are shown the data on its occurrence in line 1 derived from Washington, D. C.,

TABLE II

OCCURRENCE OF NEW POINSETTIAS FROM SELFING PLANTS IN LINE 1

| Type of Seed Parent | Number of Seed Parents | Normals | Poinsettias | Per cent. Poinsettias | Years Recorded |
|---|---|---|---|---|---|
| 2n | 16 | 1707 | 1 | 0.06 ± .040 | 1919–22 |
| 2n (Mass Planting) | 48 | 27616 | 14 | 0.05 ± .009 | 1919–21 |
| (2n + 1) | 54 | 4921 | 5 | 0.10 ± .030 | 1920–22 |
| (2n + 1) (Mass Planting) | 25 | 3242 | 0 | 0.00 | 1921 |

which has been used more than any other line in our breeding experiments. When seedlings are crowded in the field, the number of the various mutants reaching recordable age is considerably lessened. In consequence, mass-plantings are separated in the table from plantings in which the seedlings are potted up and handled individually. The number of plants so far recorded in line 1 is too small to warrant as yet any very definite conclusion in regard to the relative frequency of occurrence of the different mutants. Further data also will be necessary to decide whether or not there is any significance in the slightly increased proportion of Poinsettias and Globes (2) from $(2n+1)$ parents over that from normal $2n$ parents. It may be possible to present more significant figures at a later date when more evidence will have accumulated.

It may be mentioned that, in addition to the plants recorded in Table I which came from parents handled in the usual manner, we have secured Poinsettias and other mutants in increased numbers after subjecting parents to lowered temperatures. Due to the process of trisomic assortment, Poinsettias along with other $(2n+1)$ types also have appeared in the offspring from triploid parents (3, 4, 1).

There are apparently two factors controlling the number of new Poinsettia mutants: (1) the frequency of nondisjunction in the Poinsettia set of chromosomes; (2) the ability of the gamete or zygote to function under competition when burdened with the extra chromosome. Nondisjunction in the formation of the male gametes can have little or no influence upon the occurrence of $(2n+1Pn)$ plants since, as has been shown in the preceding section, the pollen is not effective to any considerable extent in transmitting the extra chromosome. In this respect the Poinsettia is possibly at a slight disadvantage in comparison with the Globe which is transmitted through its pollen to about 2 per cent. of its offspring. On the other hand, the survival value of egg cells or zygotes with the extra Poinsettia chromosome seems, from data in Table I, to be slightly greater than that for the Globe. The differences in these respects between the two mutants, however, are at best slight and the data are not absolutely comparable.

## FORMULAE FOR TRISOMIC INHERITANCE

The ratios in ordinary Mendelian inheritance are disomic, being based upon the facts of assortment of the homologous chromosomes which have been associated together in disomes. An entirely different series of ratios will obviously result if the chromosomes bearing the factors in question are associated in trisomes or sets of three. Before considering the detailed breeding data, it will be well to present the theoretical ratios for trisomic inheritance. This is done in Table III.

In deriving the ratios, two assumptions have been necessary: (1) random assortment of the chromosomes in the trisome, (2) failure of the extra chromosome to be transmitted through the pollen. That transmission of the extra chromosome through the pollen can be neglected is obvious from the results in Table I. The detailed pedigrees given below show that both assumptions are justified for the material treated in the present paper. A $(2n + 1)$ plant with the allelomorphic pair Aa borne by the chromosomes in a trisome will, if duplex for A, have the formula AAa. On account of the large number of homologous chromosomes that may be associated in a single set—as many as seven in a $(4n + 3)$ Globe—it has been found convenient to use subscripts in our formulae and to write a duplex plant $A_2a$. The female gametes of such a plant will be $2A + a + A_2 + 2Aa$ and the male gametes, because $(n + 1)$ pollen does not function, will be $2A + a$. Thus selfing a duplex parent should give only A plants in the $(2n + 1)$ offspring and 8A to 1a plant in the $2n$ offspring. The formulae for other genetic types are given in the table and require no further discussion.[1]

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[1] Through an uncorrected error in an earlier publication (6) the formula for the female gametes of a duplex Poinsettia was written $2P + p + pp + 2Pp$ instead of $2P + p + PP + 2Pp$.

TABLE III

TRISOMIC INHERITANCE OF AN ALLELOMORPHIC PAIR A,a IN A (2n + 1) MUTANT WHEN THE EXTRA CHROMOSOME IS NOT CARRIED BY THE POLLEN. FORMULAE FOR PARENTS, GAMETES AND BOTH 2n AND (2n + 1) OFFSPRING

| Female Parent (gametes in parenthesis) | Pollinated by | 2n offspring | | | | (2n + 1) offspring | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | $A_2$ | Aa | $a_2$ | Ratio A:a | Ratio A:a | $A_3$ | $A_2a$ | $Aa_2$ | $a_3$ |
| $A_3$ ($A_2$ + A) | $A_3$ | 1 | ...... | ...... | 1:0 | 1:0 | 1 | ...... | ...... | ...... |
| | $A_2a$ | 2 | 1 | ...... | 1:0 | 1:0 | 2 | 1 | ...... | ...... |
| | $Aa_2$ | 1 | 2 | ...... | 1:0 | 1:0 | 1 | 2 | ...... | ...... |
| | $a_3$ | ...... | 1 | ...... | 1:0 | 1:0 | ...... | 1 | ...... | ...... |
| | $A_2$ | 1 | ...... | ...... | 1:0 | 1:0 | 1 | ...... | ...... | ...... |
| | Aa | 1 | 1 | ...... | 1:0 | 1:0 | 1 | 1 | ...... | ...... |
| | $a_2$ | ...... | 1 | ...... | 1:0 | 1:0 | ...... | 1 | ...... | ...... |
| $A_2a$ (2A + a + $A_2$ + 2Aa) | $A_3$ | 2 | 1 | ...... | 1:0 | 1:0 | 1 | 2 | ...... | ...... |
| | $A_2a$ | 4 | 4 | 1 | 8:1 | 9:0 | 2 | 5 | 2 | ...... |
| | $Aa_2$ | 2 | 5 | 2 | 7:2 | 9:0 | 1 | 4 | 4 | ...... |
| | $a_3$ | ...... | 2 | 1 | 2:1 | 3:0 | ...... | 1 | 2 | ...... |
| | $A_2$ | 2 | 1 | ...... | 1:0 | 1:0 | 1 | 2 | ...... | ...... |
| | Aa | 2 | 3 | 1 | 5:1 | 6:0 | 1 | 3 | 2 | ...... |
| | $a_2$ | ...... | 2 | 1 | 2:1 | 3:0 | ...... | 1 | 2 | ...... |
| $Aa_2$ (A + 2a + 2Aa + $a_2$) | $A_3$ | 1 | 2 | ...... | 1:0 | 1:0 | ...... | 2 | 1 | ...... |
| | $A_2a$ | 2 | 5 | 2 | 7:2 | 8:1 | ...... | 4 | 4 | 1 |
| | $Aa_2$ | 1 | 4 | 4 | 5:4 | 7:2 | ...... | 2 | 5 | 2 |
| | $a_3$ | ...... | 1 | 2 | 1:2 | 2:1 | ...... | ...... | 2 | 1 |
| | $A_2$ | 1 | 2 | ...... | 1:0 | 1:0 | ...... | 2 | 1 | ...... |
| | Aa | 1 | 3 | 2 | 4:2 | 5:1 | ...... | 2 | 3 | 1 |
| | $a_2$ | ...... | 1 | 2 | 1:2 | 2:1 | ...... | ...... | 2 | 1 |
| $a_3$ (a + $a_2$) | $A_3$ | ...... | 1 | ...... | 1:0 | 1:0 | ...... | ...... | 1 | ...... |
| | $A_2a$ | ...... | 2 | 1 | 2:1 | 2:1 | ...... | ...... | 2 | 1 |
| | $Aa_2$ | ...... | 1 | 2 | 1:2 | 1:2 | ...... | ...... | 1 | 2 |
| | $a_3$ | ...... | ...... | 1 | 0:1 | 0:1 | ...... | ...... | ...... | 1 |
| | $A_2$ | ...... | 1 | ...... | 1:0 | 1:0 | ...... | ...... | 1 | ...... |
| | Aa | ...... | 1 | 1 | 1:1 | 1:1 | ...... | ...... | 1 | 1 |
| | $a_2$ | ...... | ...... | 1 | 0:1 | 0:1 | ...... | ...... | ...... | 1 |
| $A_2$ (A) | $A_3$ | 1 | ...... | ...... | 1:0 | | ...... | ...... | ...... | ...... |
| | $A_2a$ | 2 | 1 | ...... | 1:0 | | ...... | ...... | ...... | ...... |
| | $Aa_2$ | 1 | 2 | ...... | 1:0 | | ...... | ...... | ...... | ...... |
| | $a_3$ | ...... | 1 | ...... | 1:0 | | ...... | ...... | ...... | ...... |
| Aa (A + a) | $A_3$ | 1 | 1 | ...... | 1:0 | | ...... | ...... | ...... | ...... |
| | $A_2a$ | 2 | 3 | 1 | 5:1 | | ...... | ...... | ...... | ...... |
| | $Aa_2$ | 1 | 3 | 2 | 4:2 | | ...... | ...... | ...... | ...... |
| | $a_3$ | ...... | 1 | 1 | 1:1 | | ...... | ...... | ...... | ...... |
| $a_2$ (a) | $A_3$ | ...... | 1 | ...... | 1:0 | | ...... | ...... | ...... | ...... |
| | $A_2a$ | ...... | 2 | 1 | 2:1 | | ...... | ...... | ...... | ...... |
| | $Aa_2$ | ...... | 1 | 2 | 1:2 | | ...... | ...... | ...... | ...... |
| | $a_3$ | ...... | ...... | 1 | 0:1 | | ...... | ...... | ...... | ...... |

The table gives the phenotypic ratios as well as the genetic types of the zygotes resulting from the various kinds of matings. It should be remembered that ($2n + 1$) individuals are always fewer than $2n$ individuals in the offspring and, therefore, the ratios can be expected to hold only within each type unless a correction is applied for differential viability.

## COLOR RATIOS FROM POINSETTIA MATINGS

The inheritance of flower color in Poinsettias can be used as a test of the assumptions upon which the theoretical ratios in Table III have been derived. The breeding data in the present paper will be confined to two closely related main lines from Washington, D. C., Line 1 being purple and Line 2 being white-flowered. At a later date it may be possible to consider certain consistent and predictable deviations from the calculated ratios when the factors for white are derived from another source than Line 2 (4). It seems best, however, to establish the rule firmly before considering the exceptions.

Table IV gives the detailed cultures from various types of Poinsettia matings which showed segregation. While considerable deviation from the calculated ratios of Table III occurs in the individual cultures, such deviation seems to be largely random. In the summarized data in Table V, the numbers are large enough to warrant the calculation of probable errors. It will be observed that in only part of one complete ratio is the deviation from the calculated value as large as three times the probable error —and in this case the numbers are relatively small. Furthermore the various types of matings show an excess of purples about as frequently as an excess of whites.

There is only a single exception which at first might seem serious. This is the occurrence of a white Poinsettia in a cross between a duplex ($P_2p$) female and a white ($p_3$) Poinsettia. There is no doubt about the classification of this plant as a white Poinsettia. Its appearance may be tentatively explained by the exceptional functioning of a $p_2$ pollen grain.

## DISTRIBUTION OF GENOTYPES

The figures in Tables IV and V show the distribution of purples and whites, but give no direct evidence in regard to the heterozygous purples. Tests on plants in the greenhouse seem to indicate that there is a decrease in the amount of purple pigment in the flowers from $P_3$ to $Pp_2$ individuals. Since, however, the intensity of floral pigment varies from day to day in the same genetic type, probably on account of the differences in illumination and other environmental factors, it has not been found

TABLE IV

DETAILED CULTURES FROM VARIOUS TYPES OF POINSETTIA (Pn.) MATINGS SHOWING SEGREGATION FOR PURPLE (P) AND WHITE (p) FLOWER COLOR

IV (a) Analysis of duplex Poinsettia ($P_2p$). [*Cf.* also (b)].

| $P_2p \times P_2p$ | | | |
|---|---|---|---|
| Nor. | | Pn. | |
| P | p | P | p |
| 44 | 2 | 11 | |
| 52 | 3 | 19 | |
| 54 | 9 | 26 | |
| 71 | 7 | 42 | |
| 37 | 4 | 36 | |
| 76 | 10 | 21 | |
| 37 | 4 | 11 | |
| 20 | 5 | 20 | |
| 85 | 6 | 11 | |
| 84 | 7 | 31 | |
| 67 | 9 | 38 | |
| 62 | 9 | 30 | |
| 32 | 4 | 17 | |
| 47 | 10 | 29 | |
| 14 | 3 | 0 | |
| 131 | 21 | 74 | |
| 130 | 11 | 43 | |
| 86 | 14 | 9 | |
| 62 | 5 | 9 | |
| 48 | 7 | 16 | |
| 58 | 7 | 20 | |
| 18 | 2 | 7 | |
| 92 | 10 | 41 | |
| 32 | 6 | 10 | |
| 113 | 10 | 14 | |
| 67 | 8 | 26 | |
| 45 | 10 | 23 | |
| 59 | 3 | 11 | |
| 39 | 6 | 24 | |
| 64 | 8 | 23 | |

| $P_2p \times p_2$ | | | |
|---|---|---|---|
| Nor. | | Pn. | |
| P | p | P | p |
| 27 | 11 | 22 | |
| 40 | 23 | 30 | |
| 53 | 25 | 48 | |
| 63 | 27 | 31 | |
| 31 | 17 | 18 | |
| 11 | 8 | 21 | |
| 48 | 14 | 33 | |
| 42 | 17 | 30 | |
| 113 | 41 | 49 | |
| 39 | 18 | 46 | |
| 27 | 10 | 18 | |
| 27 | 11 | 17 | |
| 58 | 22 | 20 | |
| 66 | 37 | 26 | |

| $p_3 \times P_2p$ | | | |
|---|---|---|---|
| Nor. | | Pn. | |
| P | p | P | p |
| 71 | 47 | † | † |
| 57 | 24 | | |
| 74 | 49 | | |
| 49 | 28 | | |
| 299 | 164 | | |
| 286 | 81 | | |
| 406 | 235 | | |
| 62 | 29 | | |
| 660 | 383 | | |

| $P_2p \times p_3$ | | | |
|---|---|---|---|
| Nor. | | Pn. | |
| P | p | P | p |
| 8 | 2 | 8 | |
| 50 | 37 | 28 | |
| 12 | 7 | 13 | 1 |

| $p_3 \times P_2p$ | | | |
|---|---|---|---|
| Nor. | | Pn. | |
| P | p | P | p |
| 53 | 28 | 18 | 3 |
| 22 | 9 | 7 | 11 |
| 57 | 25 | 27 | 24 |
| 67 | 45 | 33 | 18 |
| 213 | 126 | 100 | 53 |

| $P_2p \times Pp_2$ | | | |
|---|---|---|---|
| Nor. | | Pn. | |
| P | p | P | p |
| 21 | 3 | 4 | |
| 74 | 28 | 39 | |
| 40 | 7 | 13 | |
| 77 | 26 | 23 | |
| 12 | 3 | 5 | |
| 32 | 18 | 21 | |
| 36 | 10 | 30 | |

| $P_2p \times Pp$ | | | |
|---|---|---|---|
| Nor. | | Pn. | |
| P | p | P | p |
| 24 | 2 | 15 | |
| 35 | 4 | 37 | |
| 46 | 4 | 24 | |
| 113 | 26 | 45 | |

IV (b) Analysis of simplex Poinsettia ($Pp_2$). [*Cf.* also (a)].

TABLE IV (*Continued*)

$Pp_2 \times Pp_2$

| Nor. | | Pn. | |
|---|---|---|---|
| P | p | P | p |
| 45 | 37 | 22 | 6 |
| 24 | 12 | 17 | 1 |
| 34 | 22 | 33 | 8 |
| 45 | 35 | 31 | 7 |
| 59 | 48 | 31 | 9 |
| 33 | 33 | 26 | 4 |
| 25 | 17 | 15 | 7 |
| 28 | 35 | 35 | 12 |
| 38 | 30 | 22 | 5 |
| 32 | 25 | 27 | 9 |
| 37 | 21 | 21 | 3 |
| 23 | 22 | 21 | 6 |
| 51 | 24 | 26 | 8 |
| 4 | 5 | 10 | 4 |
| 41 | 28 | 31 | 8 |
| 41 | 32 | 13 | 5 |
| 34 | 28 | 28 | 5 |
| 40 | 27 | 32 | 8 |
| 33 | 31 | 29 | 5 |
| 31 | 26 | 29 | 6 |
| 32 | 33 | 29 | 3 |
| 37 | 27 | 27 | 10 |
| 29 | 25 | 33 | 8 |
| 24 | 19 | 19 | 6 |
| 66 | 52 | 33 | 12 |
| 77 | 40 | 10 | 2 |
| 64 | 53 | 29 | 8 |
| 48 | 43 | 23 | 7 |
| 47 | 30 | 27 | 4 |
| 34 | 30 | 37 | 15 |
| 21 | 19 | 16 | 2 |
| 31 | 24 | 17 | 5 |
| 1 | 0 | 2 | 2 |
| 21 | 18 | 20 | 8 |
| 40 | 24 | 29 | 2 |
| 17 | 20 | 20 | 3 |

$Pp_2 \times p_2$

| Nor. | | Pn. | |
|---|---|---|---|
| P | p | P | p |
| 21 | 42 | 16 | 3 |
| 23 | 35 | 13 | 5 |
| 19 | 38 | 26 | 9 |
| 5 | 10 | 11 | 7 |
| 30 | 67 | 28 | 10 |
| 23 | 59 | 15 | 7 |
| 25 | 45 | 17 | 5 |
| 14 | 17 | 21 | 4 |
| 23 | 45 | 19 | 12 |
| 36 | 78 | 40 | 22 |

$p_2 \times Pp_2$

| Nor. | | Pn. | |
|---|---|---|---|
| P | p | P | p |
| 4 | 9 | † | † |
| 59 | 102 | | |
| 51 | 99 | | |
| 82 | 181 | | |
| 49 | 127 | | |
| 60 | 131 | | |
| 43 | 84 | | |
| 10 | 22 | | |
| 52 | 112 | | |
| 28 | 51 | | |
| 37 | 77 | | |
| 45 | 89 | | |
| 61 | 137 | | |
| 147 | 270 | | |
| 122 | 286 | | |
| 91 | 190 | | |
| 225 | 425 | | |

$Pp_2 \times p_3$

| Nor. | | Pn. | |
|---|---|---|---|
| P | p | P | p |
| 62 | 91 | 44 | 25 |
| 75 | 143 | 69 | 33 |
| 6 | 20 | 6 | 8 |
| 29 | 38 | 23 | 9 |

$p_3 \times Pp_2$

| Nor. | | Pn. | |
|---|---|---|---|
| P | p | P | p |
| 77 | 121 | 28 | 46 |
| 41 | 106 | 19 | 49 |
| 19 | 45 | 10 | 24 |
| 9 | 34 | 4 | 10 |
| 45 | 98 | 15 | 55 |
| 12 | 14 | 5 | 7 |
| 19 | 18 | 7 | 10 |

$Pp_2 \times P_2p$

| Nor. | | Pn. | |
|---|---|---|---|
| P | p | P | p |
| 43 | 9 | 34 | 1 |
| 21 | 10 | 16 | 1 |
| 100 | 23 | 26 | 6 |
| 15 | 5 | 24 | 2 |
| 65 | 17 | 20 | 3 |
| 48 | 15 | 36 | 6 |
| 17 | 4 | 11 | 1 |
| 23 | 10 | 13 | 0 |
| 18 | 4 | 15 | 1 |
| 25 | 6 | 6 | 2 |
| 49 | 19 | 49 | 3 |
| 79 | 17 | 42 | 5 |
| 71 | 21 | 45 | 8 |

$Pp_2 \times Pp$

| Nor. | | Pn. | |
|---|---|---|---|
| P | p | P | p |
| 17 | 8 | 17 | 7 |
| 24 | 12 | 10 | 0 |
| 45 | 19 | 21 | 3 |
| 52 | 24 | 19 | 4 |
| 63 | 39 | 44 | 10 |
| 108 | 61 | 74 | 10 |
| 47 | 33 | 33 | 6 |

IV (c) Analysis of nulliplex Poinsettia ($p_3$). [*Cf.* also (a) and (b)].

$p_3 \times Pp$

| Nor. | | Pn. | |
|---|---|---|---|
| P | p | P | p |
| 24 | 22 | 22 | 19 |
| 42 | 38 | 7 | 11 |
| 22 | 35 | 9 | 8 |
| 11 | 8 | 5 | 8 |
| 26 | 29 | 12 | 21 |
| 45 | 43 | 11 | 28 |

(† Seedlings from the cross Normal × Poinsettia were not grown to a stage in which Poinsettia plants could be identified since, as shown in Table I, the extra Poinsettia chromosome appears not to be transmitted to any considerable extent through the pollen.)

possible to classify the different genetic types of purple by inspection with any accuracy. If the disturbing factors could be rendered constant, we believe the presence of different numbers of genes for purple would be reflected in the flower color. With the conditions under which the plants are grown, however, it is necessary to obtain color records of their progeny in order to classify with certainty the genetic constitution of purples.

The breeding test of normals is very simple. Since mutants are not involved, the individuals to be tested can be selfed and the purple and white seedlings recorded and discarded as soon as they appear in the seed pans. Purple-flowered plants have red-stemmed and white-flowered plants have green-stemmed seedlings. Large numbers are not necessary, since purple normals are either $P_2$ or Pp, and the ratios to be distinguished are all

TABLE V

SUMMARY OF COLOR RECORDS FROM POINSETTIA PARENTS. P = PURPLE. p = WHITE
(For details of segregating cultures *cf.* Table IV.)

| Type of Pollination | Number of Seed Parents | Normals |  |  | Poinsettias |  |  |
|---|---|---|---|---|---|---|---|
|  |  | P | p | Dev./P.E | P | p | Dev./P.E. |
| $P_3 \times P_3$ | 10 | 882 | 0 |  | 263 | 0 |  |
| *Calculated* |  | *882* | *0* | ...... | *263* | *0* | ...... |
| $P_2p \times P_2p$ | 29 | 1826 | 220 |  | 692 | 0 |  |
| *Calculated* |  | *1818.7* | *227.3* ± *9.58* | *0.8* | *692* | *0* | ...... |
| $P_2p \times p_2$ | 14 | 645 | 281 |  | 409 | 0 |  |
| *Calculated* |  | *617.3* | *308.7* ± *9.66* | *2.9* | *409* | *0* | ...... |
| $P_2p \times p_3$ | 2 | 70 | 46 |  | 49 | 1 |  |
| *Calculated* |  | *77.3* | *38.7* ± *3.42* | *2.1* | *50* | *0* | ...... |
| $P_2p \times Pp_2$ | 7 | 292 | 95 |  | 135 | 0 |  |
| *Calculated* |  | *301* | *86* ± *5.51* | *1.6* | *135* | *0* | ...... |
| $P_2p \times Pp$ | 4 | 218 | 36 |  | 121 | 0 |  |
| *Calculated* |  | *211.8* | *42.2* ± *4.01* | *1.5* | *121* | *0* | ...... |
| $p_2 \times P_2p$ | 9 | 1958 | 1040 |  | † | † |  |
| *Calculated* |  | *1998.7* | *999.3* ± *17.39* | *2.3* |  |  |  |
| $p_3 \times P_2p$ | 2 | 412 | 233 |  | 185 | 109 |  |
| *Calculated* |  | *430* | *215* ± *8.07* | *2.2* | *196* | *98* ± *5.45* | *2.0* |
| $Pp_2 \times Pp_2$ | 35 | 1287 | 995 |  | 870 | 223 |  |
| *Calculated* |  | *1267.8* | *1014.2* ± *16.01* | *1.2* | *850.1* | *242.9* ± *9.27* | *2.1* |
| $Pp_2 \times p_2$ | 10 | 219 | 436 |  | 206 | 84 |  |
| *Calculated* |  | *218.3* | *436.7* ± *8.13* | *0.1* | *193.3* | *96.7* ± *5.41* | *2.3* |
| $Pp_2 \times p_3$ | 4 | 172 | 292 |  | 142 | 75 |  |
| *Calculated* |  | *154.7* | *309.3* ± *6.84* | *2.5* | *144.7* | *72.3* ± *4.68* | *0.6* |
| $Pp_2 \times P_2p$ | 13 | 574 | 160 |  | 337 | 39 |  |
| *Calculated* |  | *570.9* | *163.1* ± *7.59* | *0.4* | *334.2* | *41.8* ± *4.11* | *0.7* |
| $Pp_2 \times Pp$ | 7 | 356 | 196 |  | 218 | 40 |  |
| *Calculated* |  | *368* | *184* ± *7.46* | *1.6* | *215* | *43* ± *4.04* | *0.7* |
| $p_2 \times Pp_2$ | 12 | 1166 | 2392 |  | † | † |  |
| *Calculated* |  | *1186* | *2372* ± *18.94* | *1.1* |  |  | ...... |
| $p_3 \times Pp_2$ | 3 | 222 | 436 |  | 88 | 201 |  |
| *Calculated* |  | *219.3* | *438.7* ± *8.15* | *0.3* | *96.3* | *192.7* ± *5.40* | *1.5* |
| $p_3 \times p_3$ | 1 | 0 | 143 |  | 0 | 73 |  |
| *Calculated* |  | *0* | *143* | ...... | *0* | *73* | ...... |
| $p_3 \times Pp$ |  | 170 | 175 |  | 66 | 95 |  |
| *Calculated* | 6 | *172.5* | *172.5* ± *6.27* | *0.4* | *80.5* | *80.5* ± *4.28* | *3.4* |

(† See footnote Table IV.)

to none and 3:1. The average number of seedlings in cultures from the $P_2$ offspring of Table VI was 84.5. The smallest number was 23. Since there is only 1 chance in 1000 (8) of this smallest culture actually representing a 3:1 ratio, our classification of genotypes among normals may be considered accurate.

TABLE VI

DISTRIBUTION OF GENOTYPES AMONG OFFSPRING FROM SELFED POINSETTIAS

| Parent | Offspring | | | | |
|---|---|---|---|---|---|
| | Normals | | Poinsettias | | |
| | $P_3$ | Pp | $P_3$ | $P_2p$ | $Pp_2$ |
| $P_3$ | 23 | 0 | 10 | 0 | 0 |
| *Calculated* | *23* | *0* | *10* | *0* | *0* |
| $P_2p$ | 57 | 54 | 12 | 30 | 13 |
| *Calculated* | *55.5* | *55.5* | *12.2* | *30.6* | *12.2* |
| $Pp_2$ | 24 | 91 | 0 | 14 | 24 |
| *Calculated* | *23* | *92* | *0* | *10.9* | *27.1* |

The breeding test of Poinsettias is somewhat more tedious than that of normals if the seedlings are grown to an age when Poinsettias can be distinguished. It is not necessary to distinguish the Poinsettias, however, as a consideration of the expected ratios will show. In the first place, $P_3$ individuals which should throw all purples are to be distinguished from duplex ($P_2p$) or simplex ($Pp_2$) heterozygous individuals. The duplex heterozygous individuals ($P_2p$) throw the more purples and alone of the two ratios need concern us here. The ratio expected is 8P:1p among the normals and 9P:0p among the Poinsettias. This complete ratio assumes that as many Poinsettias as normal zygotes come to recordable age. Such an assumption has never been realized in our experience when any considerable numbers were involved. If we make the assumption of this extreme condition of an equality of normals and Poinsettias in the offspring which would give the maximum number of purples from a $P_2p$ individual, our problem then is to differentiate between an all to none and an 8:1 ratio in a population represented by half the number of seedlings in the given culture. The average number of seedlings from the $P_3$ Poinsettia offspring of Table VI was 177.8. The smallest number was 105. Assuming one half, or 52, to have been normals, there are only 2 chances in 1000 (8) that the culture under discussion represents an 8:1 ratio and that the plant from which it was derived was not homozygous ($P_3$). When it is remembered that the conventional "3 times the probable error" represents 43 chances in 1000, it is seen that our smallest culture from a $P_3$ individual stands little chance of having been wrongly classified.

The distinction between a $P_2p$ and a $Pp_2$ individual can also readily be made without recording the offspring for Poinsettias. The ratio from a $P_2p$ individual varies between 17P:1p, the extreme limit on one side assuming that the Poinsettias are equal to the normals, and 8P:1p, the extreme limit on the other side assuming that no Poinsettias survive. In like manner it may be shown that the ratios from a $Pp_2$ individual lie between the limits 2P:1p and 5P:4p. Our most difficult task possible in consequence would be to differentiate between an 8:1 and a 2:1 ratio. The classification, therefore, of the three types of purple Poinsettias by recording and discarding their young offspring from the seed pans runs counter to no mathematical principles and has given no difficulties in actual practice.

For the sake of their inclusion in Table IV all the Poinsettia offspring from $Pp_2$ parents in Table VI had their progeny classified for both Poinsettias and normals as well as the Poinsettia offspring of 18 of the $P_2p$ parents. Of the latter, 5 were $P_3$, 8 $P_2p$ and 5 Pp.

The distribution of genotypes shown in Table VI is in perfect accord statistically with the visible ratios shown in Tables IV and V. Together they form a compelling mass of evidence, we believe, that the extra chromosome in the Poinsettia mutant of Datura is a member of the set carrying the genes for purple and white flower color.

When more Mendelian characters are available it may be possible to label the chromosomes in the other $(2n+1)$ mutants by the factors which they contain. The data in the present paper, although dealing with the extra chromosome in but a single mutant, offer presumptive evidence for the specificity of the extra chromosome in all the other $(2n+1)$ mutants.

## SUMMARY

(1) The $(2n+1)$ mutant Poinsettia in *Datura Stramonium* is briefly described.

(2) The frequency of its new occurrence in offspring of $2n$ parents is about once in two to three thousand individuals.

(3) The extra chromosome responsible for the peculiarities of the Poinsettia mutant, (a) is not transmitted through the pollen or to only a slight extent; (b) is transmitted through only about 30 per cent. of the egg cells; (c) is transmitted to a slightly larger proportion of the offspring when the Poinsettia parent is pollinated from a normal or from another Poinsettia than when it is selfed.

(4) It is, therefore, concluded: (a) that the condition in the Poinsettia is similar to that previously found for the Globe mutant in that gametes with the extra chromosome are less viable than those with the normal $(n)$ number, and (b) that crossing the mutant with a normal or with another Poinsettia in comparison with selfing probably gives increased vigor and therefore increased survival value to the $(2n+1)$ zygotes which result.

(5) The theoretical ratios are given for trisomic inheritance based upon non-transmission of the extra chromosome through the pollen and upon the assumption of random assortment of chromosomes within the trisome.

(6) Both the phenotypic and genetic ratios for the inheritance of purple pigmentation in the offspring of Poinsettia parents agree closely with the theoretical ratios.

(7) It is therefore concluded: (a) that Poinsettia has its extra chromosome in the set which carries the genes for purple and white flower color, and (b) that the three chromosomes in this set assort at random.

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# THE ORIGIN OF CYCLOPEAN MONSTERS

DR. F. E. CHIDESTER
DEPARTMENT OF ZOOLOGY, WEST VIRGINIA UNIVERSITY

## INTRODUCTION

IN times past the occasional birth of monsters gave rise to strange myths of races of peoples of peculiar structure. It is quite possible that the one-legged folk described by Pliny were imagined as a result of seeing a case of monopodia or perhaps sympodia. Again, it is possible that the ancient Cyclops or Polyphemus with his one-eyed subjects was the reaction of the ancients to the cyclopean foetus.

Cyclocephalus, synapsia or cyclopia was first described by Lycosthenes in his Chronicum (1557). The specimen figured had a single eye above a normal nose. Licetus (De Monstris, p. 133, 1668) reported a monster with a mesial eye with two pupils and with a nasal proboscis above the eye. He also mentioned a Janus double monster with the same cyclopean deformity. Since the early part of the eighteenth century, many cases of cyclopia in mammals have been recorded, but in few of the cases have the descriptions been complete and the clinical data included.

Classifications of cyclopean monsters have been made by Geoffroy St. Hilaire, Ahlfeld and more recently by H. H. Wilder ('08). Stockard has shown experimentally that in the cyclopean fish we may have a regular gradation from a single median eye to an hour glass eye, and finally to two eyes close together, then to the normal two eyes. Stockard ('09) has distinguished cyclopia from the monophthalmic condition sometimes present. In this condition the single eye is in a lateral position.

## OCCURRENCE AND VIABILITY OF CYCLOPEAN MONSTERS

Among the mammals, cyclopia has been reported in man, monkey, cow, sheep, goat, pig, stag, horse, dog, cat, rabbit and rat. Cyclopia has also been recorded in birds —chick, goose, dove, duck—and in fish—salmon, skate, trout. Cyclopean monsters have been experimentally produced in the chick, frog, salamander, fish and the flatworm, Planaria.

In many of the cyclopean monsters there are no abnormalities other than those of the head. In some the mouth is normal. In man, the oldest cyclops recorded by Valenti ('94) lived seventy-three hours. In the skate described by Paolucci ('74) the age was several years, since the fish was 1½ feet long and 2½ feet wide. The fish seemed able to procure its food readily.

Yung ('01) reports a case of monophthalmia in a rainbow trout. The eye was on the left and apparently normal. The fish lived for 22 months, feeding on Tubifex. Movement was in circles. Stockard ('10) succeeded in keeping Magnesium embryos for one month in aquaria. He did not attempt to keep them longer. In cases of cyclopia in which the mouth is normal there should not be great difficulty in keeping them alive. Many of the human cyclops breathe through the mouth for a few minutes.

## General External Appearance of the Mammalian Cyclops

In cyclopia there is generally a defect of the nose, and the eye is found in the median line of the face. Sometimes the mouth is defective or even fused with the ears.

It might be profitable to consider the classification of specimens of cyclopia made by Saint Hilaire and Ahlfeld.

Geoffroy Saint Hilaire classified specimens of cyclocephalus or cyclopia as follows:

(1) Ethmocephalus.

Olfactory organs not completely atrophied. Nose represented as proboscis with two imperfect nostrils, or a single opening. There are two eyes and two eyesockets.

(2) Cebocephalus.

No nose nor representation of it. Interocular region is narrow and perfectly flat, but two eyes and two orbital cavities are present.

(3) Rhinocephalus.
In rhinocephalus the nose is represented by a proboscis inserted at the base of the forehead. Beneath this proboscis is a single orbital cavity containing two orbits more or less completely fused.

(4) Cyclocephalus.
In cyclopia proper there is a fusion of the orbital cavities and of the eyes without a vestige of a nose or of a proboscis.

(5) Stomocephalus.
In stomocephalus there is the same deformity as in rhinocephalus or in cyclocephalus; but, unlike these the lower portion of the face is affected. The upper and lower maxillary bones are very defective but the normal amount of skin is provided, so that the latter, being in excess of the needs of the lower face, hangs in folds, especially at the region of the mouth, resembling somewhat the proboscis of the rhinocephalus.

The classification of Ahlfeld,[1] which most persons now accept, is based on the fact that the specimens may be placed in a series ranging from single orbital cavity, with no eye at all, to two perfect eyes close together.

Ahlfeld's classification of cyclopean monsters:

(1) The eyes approach one another, the face is narrow, the nose is rudimentary.

(2) There is a close approach of the eyes to one another. There is a rudiment of nose, but it is still between the eyes.

(3) There is a union of the orbital cavities at their inner edge, but the eyelids still extend across the face on both sides. The nose is represented by a cylindrical body above the junction of the eye-sockets composed of the skin structure of the nose, with possibly some cartilaginous formation at the base, or pedicle.

(4) There is a complete union of the orbital cavities and a junction of the two orbits, the single eyeball, however, possessing two corneae, two pupils and two lenses. There may be an entire absence of the proboscis, but it is usually present, always above the single eye.

(5) The corneae of the single eyeball are united into a figure-of-eight space. The fused eyelids form a rhomboidal figure. There may still be two pupils and two lenses, the latter may be single but larger than common, and elongated in its transverse diameter.

(6) The cornea is not formed at all. The sclera covers the whole eyeball, and fills out the space between the two eyelids.

(7) The eyesocket is very ill developed and the orbit rudimentary or altogether absent. (Anophthalmia cyclopica.)

## THE EYE, OPTIC NERVE AND EYE-MUSCLES

Under cyclopia have been classed all gradations from two eyeballs side by side in a single orbit to an hour-glass eye, then down to a single eye, with apparently no traces of duplication, and finally to the complete absence of the eye. There may be no lens or cornea or there may be a deeply buried lens. Generally there are four eyelids. Sometimes there are two nerves unfused, sometimes the single optic nerve is formed by the fusion of the fibers just before the two eyes are reached.

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[1] These classifications are to be found in Hirst and Piersol's "Human Monstrosities." Philadelphia, 1892.

*The eye-muscles:* Owing to their position, the internal recti are generally absent. The obliques may be present. The external recti are generally present.

## THE NASAL PROBOSCIS

In many cases of cyclopia there is a nasal proboscis, generally situated above the median eye. The proboscis is generally fleshy, and may be extremely short, or as long as the ordinary nose. At its extremity is seen a fleshy opening (sometimes two) which leads into a canal containing sebaceous and mucous material. In some probosces there has been found a rod of cartilage. No olfactory nerve is found in the proboscis.

Sometimes two probosces are found. Taruffi and Vogt ('94) described a foetus in which there were two probosces one above the eye and another below it. Devaine and Robin (Ballantyne, '04) and Wilder ('08) have described similar cases in pigs in which there were both proboscis and nose. Otto described a case of sub-orbital proboscis in a lamb. Allan ('48) has described the only case that the writer knows of a human foetus with the proboscis below the eye. This specimen is a case of cyclopean otocephalus with sub-orbital proboscis.

There is a remarkable similarity between the cyclops with a proboscis and the elephant. In both cases the growth is similar. In the elephant the basal elements of the trunk and of the proboscis are separate, but subsequently unite.

## DEFORMITIES OF THE SKULL ACCOMPANYING CYCLOPIA

In man, hydrocephalus is a more frequent adjunct to cyclopia than in lower animals. When hydrocephalus accompanies cyclopia the anterior fontanelles are widely separated and the bones of the skull are thin. In cases of cyclopia unaccompanied by hydrocephalus, the bones are thick and the fontanelles are closed. (Wyman, '59.) The posterior halves of the parietals are separated, the opening being closed by a thick membrane. Generally the following bones are absent: Ethmoid, presphenoid, nasal process of the superior maxillary, lachrymals, vomer and inferior turbinated. The frontal bones are usually unfused.

The nose is represented by a fleshy teat-like process, which is generally situated above the eye. In cases in which the proboscis is absent, the ears are frequently fused (otocephalus) and the mouth is not well defined. The palate may or may not be cleft.

In the pig, according to Wyman ('59), the cranium is separated from the bones of the face and thrown upward so that the roof of the orbit is nearly vertical and extends transversely across the face. The frontal, ethmoid, vomer and nasal bones are generally absent. The superior maxillary is short and frequently recurved. Wedekind and others speak of the absence of the premaxillaries, but Wyman thinks that these are probably not absent, but displaced and represented by a pair of bones found in the snout. Wyman cites the embryological fact that the premaxillaries are developed independently from the median bud, while the maxillaries project from the first visceral arch and subsequently unite with the premaxillaries. Wyman's theory is that a cyclopean eye, projecting forward in the median line, would have a tendency to throw the premaxillary bud upward and thus prevent its union with the maxillaries. In the absence of the ethmoid, the orbital plates of the frontal meet on the median line.

In otocephalus the ears approach one another and in some specimens are united (Chidester, '14). The lower jaw is rudimentary or sometimes absent entirely. The mouth is poorly developed and may be fused with the openings of the ears. Otocephalus is extremely rare in man. One of the cases of otocephalus in the human foetus was described by Smith and Parker ('82). In this case the mouth was but 3 mm in diameter. The tongue may be rudimentary or absent. The hyoid bone may be perfect or completely absent.

The cause of otocephalus is supposed to be an arrest of the development of the lower processes (Meckel's cartilages) of the first visceral arch. Dareste held ('77, '91) that the primary cause was an arrest in the development of the cephalic fold of the amnion.

## THE BRAIN AND THE CRANIAL NERVES

In fish, Stockard ('10) noted that sometimes the brain of a cyclopean monster is only very slightly malformed. In the mammalian cyclops, however, we generally find an extremely malformed brain. In many cases there is hydrocephalus and almost invariably the cerebrum is defective. It is sometimes incompletely divided into two hemispheres, sometimes there are three vesicles (Chidester, '14), and very frequently there is no division into hemispheres. The parts which develop from the first cerebral vesicle are extremely defective. The falx cerebri is defective or absent. The corpora quadrigemina, remarkably enough, are ordinarily almost normal. The corpora striata are generally imperfect. The crus cerebri is generally single. The fornix, septum lucidum and corpus callosum are generally absent, though Banchi ('05) reported a case in which they were normal and the corpora striata were present in good condition. The third and lateral ventricles are commonly fused together. This was the case in Banchi's specimens, though both fornix and corpus callosum were present. The epiphysis is frequently absent, but the hypophysis is almost always present.

There is great variation in the occurrence of an optic nerve. In the case of the absence of the eyeball, the optic nerve is generally absent. With fused eyes, the optic nerves may be separate; or there may be a fusion until just before the eyeballs are entered; or there may be but one nerve. Sometimes well-developed eyeballs are not accompanied by the formation of a nerve. The olfactory nerves are frequently absent in almost any stage of cyclopia. The third, fourth and sixth nerves are frequently small, but generally present. The other cranial nerves are generally present.

The Circle of Willis has been figured in but few cases of cyclopia on record. Cleland ('77) reports two cases of cyclopia in the pig in which a mesial artery instead of a pair of internal carotids pierced the dura mater and joined the basilar. Phisalix ('89) gives drawings of the brains of a child, two sheep and a dog, in which he figures the blood supply of the brains. Black ('13) figures the encephalic arteries of a case of cyclopia in man, in which he shows that the superior and posterior inferior cerebellar arteries were all quite small and arose from the basilar, while the anterior inferior cerebellar arteries branched in both directions. Black also indicated that the posterior portion of the cerebral vesicle on the left side was supplied wholly by the posterior cerebral branch of the basilar artery.

As in uncomplicated hydrocephalus (Blackburn, '07, 07a) the blood vessels may be present in normal position, although quite small, as instanced in several cases including one described by the writer ('23).

*Histological structure:* Microscopical study of some of the brains serves to aid considerably in the settlement of questions regarding the fiber tracts and nerve connections. One of the most interesting studies thus made is that of Black ('13).

Duckworth ('08) studied the spinal cord of a defective pig in which the brain was perfectly symmetrical, consisting of medulla, pons and cerebellum, with the structures connected with those parts. The cerebellum capped the pons as in a specimen recently described (Chidester, '14). The tracts of the cord were shown as clearly as in the control and Duckworth thinks that this indicates a strong support for the theory of the laying down of the pyramidal tracts in situ. In most cases of cyclopia the descending tracts are absent.

## DEFORMITIES OTHER THAN OF THE HEAD ACCOMPANYING CYCLOPIA

As previously shown, malformations of the head, such as otocephalus, hydrocephalus, anencephalus, hare-lip, absence of either of the jaws, or the presence of the so-called proboscis, are frequent in cases of cyclopia.

Deformities of other parts of the body may occur in association with cyclopia. Some of these, such as polydactyly or club foot, seem to be inherited.

It is worthy of note that deformities in the median line are of frequent occurrence. There may be an absence of one of the paired visceral organs; or there may be inversion of the viscera (Taruffi and Vogt, '94). Spina bifida is common (Panum, '80). Polydactyly seems to be an exceedingly frequent concomitant with cyclopia (Earl, '00). Exomphalus and umbilical hernia have been reported. Diaphragmatic and abdominal hernias are fairly common (Ballantyne, '04). The reproductive organs in the female cyclops are frequently malformed, there being such deformities as uterus bicornis duplex and septate vagina (Renner, '89).

## EXPERIMENTAL PRODUCTION OF CYCLOPIA IN THE LOWER VERTEBRATES

A number of the early workers on the development of the egg of the common fowl secured occasional cases of cyclopia by varying the temperature of the incubator, shaking, varnishing, electrical stimuli, reducing the supply of oxygen, etc. Experimental teratogenesis established amniotic defects as the most probable cause of the occurrence of the monstrosities and it was the belief of Dareste that cyclopia was due to the arrest of development of the anterior cerebral vesicle, the result of the premature closure of the cerebro-spinal groove.

Féré ('93–'03) not only repeated the experiments of

Dareste and others, altering temperature, traumatism, mechanical vibration, colored light and varnishing, but he tried the effects of gases which might penetrate the shell, surrounding the eggs with an atmosphere of turpentine, musk, mercury, phosphorus, ammonia, ether, chloroform, alcohol and tobacco, before incubation. He also injected substances in solution into the albumen of the egg. He used solutions of salt, glucose, glycerine, potassium iodide, potassium and strontium bromide, peptone, creatinine, xanthocreatinine, cantharidine, nicotine, sulphate of strychnine, many alcohols, acetone, toxins, blood, morphine, atrophine, atropine, cocaine and venine. In all Féré's work, control experiments were made and large quantities of eggs were used.

Féré secured omphalocephaly, atrophy of the head, double heart, atrophy of the tail, cyclopia and other monstrosities by means of almost all the injected substances; and secured a large quantity of monsters by the subjection of the eggs to gases and by agitation. He found that the intensity and duration of action of the disturbance caused a greater number of monsters, but he did not find that any specific influence was responsible for a particular monstrosity.

The introduction of anesthetics and toxins into the eggs by Féré was a long step in advance of any previous work in experimental teratogeny. Dareste decided from his experiments that the arrested development of the embryo was the cause of the defect in the amnion which acted by pressure on the embryo. Féré, on the contrary, showed that the same anomalies may occur both with and without arrest in the development of the amnion. Féré seems to be of the opinion that a change in nutrition is the cause of monsters. In speaking of Féré's work, Ballantyne ('04) states his belief that the two hypotheses may be combined and suggests that in the case of the human ovum, there may be a defect in nutrition which arrests the growth of the amnion, leading to pressure of the amnion and subsequent arrest of the development of the embryo. Ballantyne holds that in cases where the amnion is not arrested and the embryo is malformed, the general cause, nutritional or otherwise, came into action after the amnion had been formed, and acted in some other way on the embryo.

Born ('97) secured cyclopia in the frog by splitting the head sagitally after the formation of the medullary plate and then readjusting the halves.

Spemann ('04) ligatured salamander eggs obliquely to the first plane of cleavage and secured embryos with double heads, one of which was frequently cyclopean.

Lewis, in 1905, secured cyclopean Funduli by pricking the anterior end of the embryonic shield. In many cases the prick destroyed the nose only. Mall, who reports the work ('08), holds that this shows that it is the absence of the tissues that allows them to come together and unite, and that a rudimentary brain is unnecessary in cyclopia. (See Lewis, '09.)

In 1907 Harrison produced cyclopia by the entire removal of the brain in frog embryos. (Mall, '08.)

Stockard found ('07) that the eggs of Fundulus developing in a solution of $MgCl_2$ in sea water developed cyclopic deformities. Later ('09) he advanced the theory that the action of the magnesium was anesthetic, inhibiting the optic outpushings. Later work by the same author ('10) showed that alcohol and other anesthetics produce a large per cent. of cyclopean and monophthalmic Funduli. Chloretone, chloroform and ether are more general in their action but many cyclopean fish are produced by them. Stockard's work served to show that normal eggs may be caused to develop into cyclopean monsters by chemical disturbance. He has also carried out experiments on the eggs of the fowl and produced deformities in chicks as did Féré.

McClendon showed conclusively ('12) that cyclopean monsters may be produced in Fundulus by many different substances such as KCl, NaCl, NaOH and cane sugar, thus disproving earlier beliefs in the specificity of substances such as salts and anesthetics. Newman, who had previously secured various types of monstrosities by the *hybridization* of fishes (1908 et seq.), suggested in 1917 that the *axial gradient* theory of Child, "a quantitative one, depending on the rate of metabolic activity, is the true explanation of teratological development in axiate forms." The anomalies included numerous types of defects of eyes and ears. It is worthy of note that the "axial gradient" theory, long unrecognized, is now being accepted pretty generally as the explanation of varying anomalies. (Child, "Individuality in Organisms.")

Loeb (1915) showed that eye defects result in fishes reared in darkness and under low temperature conditions.

Werber ('15) produced cyclopic Funduli by means of butyric acid and acetone and suggested that monstrous development was due to metabolic toxemia.

Kellicott ('16) showed that low temperature produced abnormal development, including cyclopic deformities, in the fertilized eggs of Fundulus heteroclitus. He concluded that the cause of the abnormal development was a disturbance of the normal organization of the ovum, and suggested his "disorganization" hypothesis in place of the nutrition and metabolism hypothesis of Mall, Stockard, Werber and Loeb.

Gladstone and Wakely ('20, '23) incline also to the belief that cyclopia and agnathia, like hare-lip and cleft palate, are attributable to defective nutrition at the proper stages.

Whether there may not also be a *germinal factor* in some cases of the cyclopic deformity is not yet shown. Wilder ('08) inclines to the belief that there is such a germinal factor.

It was shown in a most striking way in the case of monophthalmia in one of twin fishes described by the writer (Chidester, '14), that an anesthetic may produce a defect of the eyes in one of identical twins, without in any way injuring the other fish. If the defect had been a germinal one, it is likely that the identical twins would have both been abnormal. The not infrequent occurrence of identical deformities in mammalian twins may of course be readily explained on the basis of nutritional disturbance and to that idea the writer is quite ready to subscribe.

Child ('11) discovered in 1909 that he could produce cyclopia in the Plathyhelminth, Planaria by means of anesthetics such as chloroform, alcohol, chloretone and ether, and it was due to his suggestion that the writer engaged in the use of these substances in connection with Fundulus experiments. All gradations of the monophthalmic and cyclopic order were produced with ease in these remarkable experimental animals so long used by Dr. Child.

Since we have suggested the theories of possible origin of cyclopia, it will be well to take up some of the older theories and elaborate upon them.

## THE ORIGIN OF CYCLOPEAN MONSTERS

The history of the conjectures regarding the origin of cyclopean monsters is essentially the same as that of the origin of other teratoma.

The early theories of the supernatural origin of monsters were followed by theories based on an incomplete knowledge of the parts played by the semen, menses and ova in the development of the embryo.

Hybridity was held to be the cause of monsters until Bianchi, in 1741, pointed out that when the product of human gestation had a rough resemblance to an animal form, this resemblance might be due to a fetal disease or the product itself might be a mole or retained portion of the placenta. Duval advanced the theory that sterility between animals of different species may be due, not to an absence of impregnation, but to such an abnormal development subsequent to impregnation as to cause arrest by its very abnormality.

Passing over the theories which are not tenable in the light of our present knowledge of pathology, we may profitably consider a few of the more plausible explanations of the origin of mammalian cyclopia.[2]

### (*a*) *Mechanical Theory*

Dareste held ('77) that cyclopia was caused by the compressing action of the head folds of the amnion.

Mall ('08), from an extensive study of early human embryos, has come to the conclusion that pathological embryos are due to the faulty implantation of the ovum, resulting in faulty nutrition.

Hannover (Ballantyne, '04) believes that in cyclopia the primary defect is due to an imperfect formation of the prechordial part of the base of the skull.

### (*b*) *Diseases of the Foetus*

With respect to the foetus, following Ballantyne ('02, '04), we may consider (1) diseases of the foetus itself; (2) diseases of the foetal membranes which set up abnormal conditions in the embryo or foetus.

(1) Hydrocephalus was very early attributed as the cause of anencephaly. Beclard, 1816, advanced the theory that dropsy is one of the most frequent diseases of the foetus, and that it might give rise to a hydroencephalic hernia. He also held that the destruction of the olfactory nerve would cause the atrophy of the ethmoid bone and the union of the two eyes. This for Beclard explains cyclopia, otocephalus and paracephalus.

Bruce ('96) regards as a separate or contributing cause of cyclopia a limited pachy- and lepto-meningitis. Blackburn ('07a) believes that uncomplicated hydrocephalus is caused by an inflammation of the ventricles.

It is possible that in the mammals, where hydrocephalus is a frequent occurrence in cyclopia, hydrocephalus is a contributory cause. Since in the non-cyclopean hydrocephalic brain there are many anomalies of the Circle of Willis (Blackburn, '07), it is exceedingly difficult to determine the part which any abnormality of the blood vessels in cyclopean hydrocephalus may have played in the production of the monstrosity. It is hoped that the study of a large number of specimens may throw some light on this point.

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[2] The historical portions of this account are compiled from Ballantyne. ('02, '04).

(2) In the discussion of the diseases of the foetal membranes as possible causes of monstrosity, the amnion has been the center of attention. Schroeder believes that syphilis may cause hypertrophy of the villi of the chorion.

Amniotic disturbances as a cause of cyclopia has many champions. Dareste holds that cyclopia originates as a result of amniotic compression which causes an arrest of development of the anterior cerebral vesicle. (Dareste, '77, '91) Rabaud ('01), however, showed that in artificially produced cyclopia in the chick, in which there was evidence of amniotic compression, the morbid changes are not those of true cyclopia, but rather of states resembling cebocephaly or approximation of the eyes. Ballantyne ('04) points out that the amniotic influence may be due to disease, poisons or mechanical states, which may delay the formation of the amnion. One strong point against the amnion as a factor in producing cyclopia or any other monstrosity, is the fact that the *formation of the amniotic sac precedes that of the embryo.*

### (*c*) *Maternal Diseases*

If syphilis produces hydrocephalus, it is quite possible that cyclopia is produced by the hydrocephalus and thus indirectly by disease. It is equally possible that other diseases in the mother may cause the inhibition of the development of whatever system is being developed at the time of the onset of the disease.

It is highly probable that disturbances of the functions of the *organs of internal secretion* are responsible for many of the foetal monstrosities.

### (*d*) *Pathology of the Germ*

In the light of the work of Bardeen ('07, '11) and others, we must admit that a teratogenic condition may be produced in the embryo by subjecting the ova or the spermatozoa to external agents. It is not a very great step to the supposition that there may be an inherited teratogenic condition of the blood which is the cause of the malformed development of the embryo, and it is even less hard to believe, in the light of what we know of the occurrence of the same malformations in several generations of the same family, that the teratogenic conditions may exist in the germinal or preembryonic state, before fertilization. The causes of these teratogenic conditions may be mechanical, chemical or toxic. In the discussion of experimental work done upon various groups of animals, it is often forgotten that after the stimulus of the spermatozoon, the development is truly subject to the influences of environment, whether the embryo be in a shell outside the body of the animal, or whether the development takes place in the body of a mammal, with an amnion and a placenta.

It might be profitable to consider a few of the cases in which in mammals a possible predisposition—germinal factor if you will—caused the birth of more than one cyclopean monster to the same mother.

Caradec recorded a case in which a woman gave birth to a female cyclops, then to three well-formed males, and then to three females, of which one had hydrocephalus, the second hare-lip and cleft palate, and the third cyclopia (Ballantyne, '04). Brotherston recorded a cyclopean lamb which was one of thirty similarly deformed, all the offspring of one ram (Symington & Woodhead, '88).

It is possible that all the cases recorded in man may be traced to similar methods of living during the early stages of pregnancy, or it is of course possible that either *ova* or *spermatozoa* were defective. We do not know in the case of the cyclopean lambs whether there were more than two or three females which gave birth to the cyclopean lambs sired by the same ram. We know nothing of the conditions of grazing of the flocks, existence of possible abortifacient weeds, or, what may be even more to the point, the relationship of the females who bore the monsters.

It is not necessary to dwell in this connection on the other monstrosities which are born in succession to the same parent. Suffice it to say, certain fish were found by Born ('97) to be prone to yield double monsters, the tendency remaining almost constant and but little influenced by a difference in the source of the spermatozoa. Féré found that some hens were prone to lay double yolked eggs. Stockard's legless lambs ('07 and '09) were sired by the same ram and one of the mothers bore two legless lambs at the interval of a year. Stockard holds ('09) that in this flock the occurrence "is probably due to germinal variations, either within the mother or father or both." In monsters it is well known that the female sex predominates. Possibly the same factor which causes the mammalian ovum to develop into a monster may stimulate the action of a sex determiner. Present chromosome theories do not admit this possibility.

### (*e*) *Drugs and Anesthetics*

Porak has shown ('94) that mercury, phosphorus and arsenic may cause abortion in the guinea pig. Arsenic is a particularly strong abortifacient, causing placental hemorrhages. Lead does not produce abortion. Observations have been made by various scientists on the offspring of workers in mercury, lead, phosphorus and arsenic and the general conclusions seem to be that they act similarly to syphilis, in producing abortions, malformations of the brain and visceral lesions. There is apparently paternal as well as maternal transmission. No cases of cyclopia have been directly traced to these causes.

It has been clearly shown by Nicloux ('08) that in guinea pigs, ether, chloroform and alcohol can pass from mother to foetus. The effects of these anesthetics on the chick and the fish have been previously discussed. For centuries, monstrosities have been attributed to the drunkenness of the parents. Early work was largely conjectural, and based on statistics, which were frequently manipulated to suit a preconceived idea. More recent statistical work, such as that of Sullivan and of Pearson, shows a little better science, but neither of these workers has proved his point.

Mairet and Combemale ('88) secured from an alcoholized bitch seven puppies, four of which were dead, two healthy with but little intelligence and the last physically and mentally backward. The offspring from this animal when bred with a normal male were deformed. One had clubfoot, another had muscular atrophy of the hind legs.

Palazzi, on the contrary, found ('01) that in rabbits injected with alcohol during pregnancy, the five which became pregnant, of seventeen in all, gave birth to twenty-four fetuses all of them living and well formed.

Hodge found ('03) that the offspring of alcoholized dogs were deformed and non-viable.

Laitinen found ('08) that the offspring of alcoholized guinea pigs and rabbits were frequently stillborn.

Nice, feeding alcohol, nicotine and caffeine to white mice and subjecting others to the fumes of tobacco, found ('12) that of 707, none were deformed nor born dead. The young of the alcoholized mice weighed more than the others.

Stockard ('12, '13, '16) has shown that in guinea pigs it is possible to induce the appearance of deformities among the young of parents subjected to the fumes of alcohol daily for six days per week. He secured various stages of eye-defects from anophthalmia to monophthalmia. The descendants of some of the young were in enough cases defective to indicate that there had been an injury to the germ cells.

## SUMMARY

(1) Cyclopia occurs in mammals, birds and fishes.

(2) The mammalian cyclops does not live long on account of inability to breathe.

(3) All gradations from a single median eye to an hour-glass eye and finally to two eyes close together are classed as of the cyclopean order.

(4) The optic nerves present corresponding degrees of abnormality, there being sometimes no nerves, again perhaps a single nerve, and finally two nerves forming a more or less complete chiasma.

(5) The internal recti muscles are generally absent. The obliques may be present. The external recti are generally present.

(6) The nasal proboscis frequently accompanies cyclopia. It is fleshy and is supposed to be the fleshy part of the nose, the cartilaginous part of which is prevented by the median eye from assuming its normal position.

(7) In mammals, cyclopia frequently occurs with hydrocephalus, the skull is greatly distorted. In cyclopia unaccompanied by hydrocephalus, the frontal bones are fused; the ethmoid, nasal, superior maxillary, lachrymal, vomer and inferior turbinated are absent.

(8) The first cerebral vesicle is the one most affected in cyclopia. The cerebrum is frequently a single vesicle with the lateral ventricles fused with the third. The corpora quadrigemina come from the mesencephalon and are generally normal. The pons, medulla, cerebellum and fourth ventricle are usually normal. All the cranial nerves back of the fourth are generally normal. The Circle of Willis may be normal.

(9) Deformities of parts of the body other than the head are frequent accompaniments of cyclopia. The malformations most frequently occurring with cyclopia are spina bifida, polydactyly, inversion of the viscera and abdominal hernia.

(10) Cyclopia has been produced mechanically in the flatworm, fish, amphibian and bird; by hybridization in the fish; by temperature change in the fish and the bird; and chemically in the flatworm, fish, bird (chick) and mammal.

(11) Cyclopia in mammals, as in lower forms, is due to

the action of some physical or chemical agent at the period just before the optic vesicles are pushed out. The extreme susceptibility to external influence manifested by the developing sense organs, particularly the eyes, renders deformities of the cyclopic order of quite surprising frequency in experiments with lower vertebrates, and the theory is advanced that disturbance of the metabolism of the mother due to disordered secretion of the hormones may be a contributing cause of numerous mammalian deformities.

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# THE THRESHOLD OF FERTILITY IN RATS AND ITS RELATION TO DIET DEFICIENCY[1]

DONALD MACOMBER, M.D.

IN 1920 and 1921, working at the Bussey Institution, we carried out certain experiments with rats to determine the effect of deficient diets on breeding and to see whether we could produce sterility by this method. The work was suggested to us by certain effects of deficient diet as reported by Dr. E. V. McCollum, of Johns Hopkins University. He had found that rats on deficient diets not only failed to make satisfactory growth but often failed to reproduce.

The diets which he used were as a rule quite deficient in one or more important factors and for that reason were hardly comparable to diets which might be taken by animals or human beings in a state of nature. For our purpose it seemed wiser to try to devise deficient diets which should fall in this latter class. With the aid of Dr. McCollum our diets therefore were designed so as to be deficient in a given dietary factor but not so deficient as to interfere with growth. An analysis of the diets is given in Table I.

TABLE I.

COMPOSITION OF DIETS

| Stock Diet. | | Normal Diet. |
|---|---|---|
| Hominy | 33.25 | |
| Rolled oats | 33.25 | |
| Meat scrap | 22.0 | |
| Skim milk powder | 11.0 | |
| Salt | 0.5 | |

In addition, unlimited amounts of special "dog" bread with analysis; Carb. 65 per cent., prot. 15 per cent., Fat 7 per cent., calc. phos. 6.7 per cent., Fibre, etc. 6.3 per cent.

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[1] This work was aided by a grant from the Elizabeth Thompson Science Fund.

TABLE I.—COMPOSITION OF DIETS (*Continued*)

| Diet A. | | Low in Calcium. |
|---|---|---|
| Whole wheat | 67.5 | |
| Casein | 15.0 | |
| Whole milk powder | 10.0 | |
| Sodium Chlorid. | 1.0 | |
| Inert substance | 1.5 | |
| Cod liver oil | 5.0 | |
| **Diet B.** | | **Low in the Fat Soluble Factor.** |
| Rolled oats | 40.0 | |
| Gelatin | 10.0 | |
| Casein | 5.0 | |
| Salt mixture (McCollum) | 3.7 | |
| Dextrin | 40.3 | |
| Cod liver oil | 1.0 | |
| **Diet C.** | | **Low in Protein and Calcium.** |
| Wheat whole | 60.0 | |
| Sodium chlorid. | 1.0 | |
| Inert substance | 1.5 | |
| Dextrin | 32.5 | |
| Cod liver oil | 5.0 | |
| **Diet D.** | | **Generally Deficient Diet.** |
| Wheat bran | 20.0 | |
| Wheat middlings | 14.0 | |
| Ground oats | 13.0 | |
| Corn meal | 9.5 | |
| Gluten meal | 10.0 | |
| Meat scrap | 12.0 | |
| Alfalfa meal | 20.0 | |
| Powder chalk | 1.5 | |

The result of these early experiments bore out what we had anticipated and we did actually produce a certain number of completely sterile animals. Post-mortem examination showed that there were no gross anatomical abnormalities, and sections of ovaries and testicles failed to show any noteworthy changes in these organs. We had used for our work a strain of Albino rats which had been inbred by Dr. Helen D. King, of the Wistar Institute, for 33 generations of brother and sister mating. She had found that inbreeding at first much reduced health and fertility, but that if the individuals chosen for continuing the strain were selected for vigor the fertility and health of the stock became restored, though at a somewhat lower level than for controls. In order to accumulate a sufficient number of these rats for our experiments it became necessary to continue the inbreeding. In this way we accumulated records of a good many matings of rats on a normal diet (the so-called "stock diet"). We found that there was the greatest possible difference in the fertility of the various individuals. For instance, the matings of certain individuals were practically invariably successful, whereas in other cases only one or two out of a number might be positive, and there were all degrees of variation between them. We were forced, therefore, at the outset to the conclusion that even in this homozygous strain individuals varied as to fertility as well as in other characteristics.

Having accumulated a sufficient stock of young and fully mature animals of this inbred strain we proceeded to submit them to the various diets already referred to in Table I. Our procedure with the adult animals was first to test their fertility, then place them on diet for one month and re-mate. Before a mating was considered negative it was allowed to continue from six weeks to two or more months. The young animals were put upon a diet directly after being weaned and were allowed to grow to maturity upon it before being mated. In our first experiments all matings were between rats which had been submitted to the same diet. When we came to check up results it seemed that we had produced a good deal of sterility, as many of the matings so made up were negative. In order to be certain of our ground, however, we first re-mated each "sterile" animal with a highly fertile rat which had been raised and tested on the stock diet. The result of these re-matings in many cases was immediate reproduction. In 37 cases it proved that both of the animals supposed to have become sterile through diet and which were unable to have young together proved to be promptly fertile when re-mated with these new and highly fertile partners. In many other cases one of the original pair proved fertile.

It seemed impossible to explain these results with any knowledge at our command, and we were forced to formulate our hypothesis of relative fertility. The problem was how to explain the fact that two individuals who might have a sterile mating together would promptly reproduce with other partners. They must have been fertile in some degree all the time, but apparently their degrees of fertility were not sufficient when combined to produce young, and yet that of each was sufficient for reproduction with a more highly fertile partner. We adopted for trial a hypothesis which in brief was as follows—that the fertility of a mating could be expressed as the product of the fertility of the individuals concerned, and that if this mating fertility were below a certain level which we called the "threshold for reproduction" no young would result, but that if it were above this level the mating would be positive. We advanced this hypothesis in a tentative way, for we realized that we had not sufficient experimental proof to confirm it in any degree, but it seemed sufficiently probable to warrant collecting a large number of breeding records with which to test it out. As controls we had the records of 1,381 rats bred by Dr. Castle on stock diet. They were of many varieties as far as genetic constitution is concerned and were as a whole highly fertile. Out of 1,172 females 1,109 were fertile, 4 were completely sterile, 15 doubtful and 44 were killed or died from disease or other cause. Of 209 males 190 were fertile, 7 sterile, 9 doubtful and 3 died or were killed. The fertility of this stock was therefore very high and is to be contrasted with that of the inbred rats where the percentage of sterile and doubtful cases was very much higher. As stated above, the effect of diet upon these inbred animals had been still further to reduce fertility and to increase the amount of sterility. We have records of 622 matings of these inbred rats. Some of these matings were between rats whose fertility had been artificially lowered by deficient diet, some were between inbreds naturally of lowered fertility, and some with proved animals from the control stock; thus every possible combination was made in our matings. These records are given in condensed form as an appendix to this paper. An analysis of them shows that there were 46 rats which were mated 5 or more times; 19, 4 times; 33, 3 times, and 42 with only 1 or 2 matings each. If we for the moment disregard all those rats which had less than 5 matings, and classify these 46 animals according to the percentage of successful matings which each had, we can get perhaps a rough indication of their comparative fertilities. There were only 2 where 80 per cent. or better of the matings were successful; in 5, between 60 and 80 per cent. were successful; in 10, 40 to 60 per cent.; in 10 more, 20 to 40 per cent., and in 5, less than 20 per cent. In addition to these 13 other animals proved to be completely sterile. This immediately gives us a rough method of classifying the fertility of these individuals, but it will of course give a false picture to this extent, namely, that the other partner of each mating must be taken into consideration, and that a negative mating with a rat all of whose matings are equally negative should not be counted as necessarily detracting from the fertility of the first individual. In other words, the breeding record of every individual must be considered in conjunction with that of the individual with which he has been mated, and these latter in turn with the records of those other rats with which they have been mated. It will be seen that it is possible by a method of trial and error and repeated revaluation gradually to approximate figures which will represent the degree of fertility for all individuals concerned. It is convenient to make these estimations as percentages, and when fertilities are so estimated it is found that in practice the figures so obtained can be used to calculate the fertility of a mating and to predict whether it will be a productive or an unproductive one.

The manner in which the breeding records (see the appendix) were used to calculate the approximate fertilities of the individual rats was, as has been said, by a process of comparison and constant revaluation. A few examples will give the method by which these estimated fertilities were derived. First, let us take the record of rat No. 1. He was mated with 3, 80, 5, 24, 26, 68 and 32F. All the matings were positive with the exception of the one with 24. Rat No. 1, therefore, is obviously of high fertility, but the degree of fertility can not be calculated without consulting the records of all these animals, for it might be that, with the exception of 24, they were all of very high fertility, in which case we would get no help as to the degree of fertility of No. 1. Similarly, it would influence our judgment as to No. 1 to find that 24 was of reasonably high fertility or the reverse. A glance at the records of 3, 80, 5, 26, 68 and 32F shows them to be of varying fertility, some, such as 68 and 32F, are of rather low fertility, while 3 and 5 are of average fertility. Since all their matings with No. 1 were successful that makes our estimate of No. 1's fertility all the higher. The record of 24 is poor (see appendix); in fact so poor as not to detract materially from our estimate of No. 1. We are safe, then, in considering No. 1 to have a fertility between 90 and 100 per cent. One or two other examples will suffice. Rat No. 1, as indicated by the letter "s," was on stock diet. Rat No. 17 was a male on diet C. After having been on the diet for a sufficient period of time it was mated with 13, which had been on the same diet. Their mating was unsuccessful. They were each then mated with animals of proved high fertility from Dr. Castle's vigorous strain, which had been on stock diet. Rat 13 never had a successful mating, but 17 did have 1 positive mating out of 5 such re-matings. The fertility of 13 can not be definitely assigned, but it is certain that it was much lowered and the probability is that it was so low as to render this rat physiologically sterile. In the case of 17 it is obvious that there was some degree of fertility. It is difficult to make an accurate estimate, however, until we have discussed further results and used our theory as to the threshold value for reproduction.

Proceeding in the manner which has just been indicated, and with constant reference back to the actual breeding records of the various rats, it was possible in many cases to give approximate figures representing the individual fertility of these rats. The next step was to substitute the values so deduced in our mating formula. We had already been able to calculate approximate values for the fertility of individuals, but we now wished to be able to assign a value to the fertility of a mating. This mating fertility we postulated as the product of the individual fertilities of the two partners. We chose this formula in preference to one derived from the sum or the average of the individual fertilities, since it comes nearer to expressing the truth of the actual results and since it is the only formula which gives practical aid in calculating individual fertilities and predicting results. It must of course be understood, however, that at this stage of our knowledge such an assumption is quite arbitrary. Putting the formula into mathematical shape, it becomes $x \times y = m$, where x is the fertility of the male, y of the female, and m of the mating, all expressed in percentage form. When the calculated values for x and y are substituted in this formula a simple multiplication of the two gives us the fertility figure for that particular mating. This procedure was carried out wherever the individual fertilities were known, and the values for the mating fertilities so derived were arranged in a series. It was at once discovered that all the values for those matings which had been productive were above a certain figure, and the values of those which were negative were below this figure. This figure proved to be in the neighborhood of .50 or 50 per cent. We gave it the name of the Threshold for Reproduction. There were, however, certain exceptions to the general rule, but it was found that they were grouped closely about this level. In order to explain these anomalous cases we put forward the suggestion that instead of a rigidly fixed value, such as 50 per cent. for the Threshold, there is rather a doubtful zone extending above and below it. With this change we can now state definitely that all matings above the doubtful zone were positive, and all matings below were negative. With our present rough methods of estimating individual fertilities it is impossible to predict certainly whether a given mating will be positive or negative if it falls within this zone.

If this theory of the threshold value for fertility is accepted as a working hypothesis it proves to be of the greatest help in further correcting some of the estimations of individual fertilities. As an example of this practical utility, let us consider the records of rats 72 and 73 (see appendix). When they were mated together no young were produced, but when each was remated with a partner of proved high fertility reproduction occurred at once. In making use of our formula let us first assume that 72 and 73 were of equal fertility. If subsequent matings make it probable that this was not the case it will be very simple then to make the necessary changes. Since x equals y, which is the mathematical way of recording our assumption of equal fertilities, the formula become $x \times x = m$, and the figure for m must have been below 50 since no young were produced. Solving this equation, x equals the square root of a number less than 50, or x is less than .70. This figure could not, however, have been less than .50 because in that case the re-matings with 100 per cent. fertile animals would have been negative, whereas we have seen that they were positive. Then, on the assumption that their fertilities were equal, the individual fertility of each becomes somewhere between .50 and .70, and would probably be in the neighborhood of .60; but a glance at their subsequent mating records makes it evident that their fertilities were not equal since after being mated together 72 had 2 other positive matings, while 73 had 2 negatives and 2 positives. From this record 72 must be materially more fertile than 73. The product of their mating fertidities can not exceed .50 because if it had their original mating would have been positive. On the assumption that they were of equal fertility we assumed a figure in the neighborhood of .60 more or less. If we give a higher value to 72, 73 must be therefore correspondingly less and yet the value for 73 can never be below .50, because if it were the animal would have been permanently sterile. A figure for 73 somewhere between .50 and .60, say .55, is probably not far from the truth. This would give a figure for 72 of about .65 since their product must not exceed .50.

No further attempt will be made in this paper to elaborate the application of this theory of the Threshold Value for Reproduction to the practical assigning of values for the fertility of individual animals from their breeding records, but enough has been said to indicate the method and to suggest its utility when applied in practice. By its use it will be seen that if the individual fertilities of two animals have been calculated from previous breeding experiments the result of their mating together can be predicted. For instance, the fertility of 99 from its first 6 breeding records can be calculated to be in the neighborhood of .55; similarly, that of 100 to be about the same figure. It could be confidently predicted that a mating between these two would be completely sterile and such proved to be the case. Similarly for the mating between 99 and 108. In the breeding tables in the appendix are given complete records and there also may be found estimated values for the individual fertilities where it was possible to obtain them.[2]

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[2] There are several variations of the mating formula $x \times y = m$ which are useful in determining values for either x or y. Where x and y are equal the formula becomes $x^2 = m$, or $x = \sqrt{m}$ and where either x or y stands for the fertility of a proved 100 per cent. fertile animal the formula becomes either x or $y = m$. In making calculations it is usually simpler to assume that the Threshold is .50, hence if a given mating has been productive the value for m must have been higher than .50 and conversely if it has been negative the value will have been below .50. These considerations are often extremely useful in calculating values for individual fertilities. It will be seen of course that they are in no way to be interpreted as having a high degree of mathematical exactness.

These estimated values have been gathered together in Table II and arranged in five columns. The first column is made up from the 1,300 odd breeding records furnished us by Dr. Castle as controls. These were between vigorous animals raised and mated on stock diet. Their genetic constitution was of the most varied type. The second column is made up of all the inbred Albino rats on stock diet of which we had definite records. The last three columns show the effect of various deficient diets upon the fertility distribution among the inbred rats. The third column is for adults which had been raised to maturity on stock diet and whose fertility had already been proved before they were submitted to the deficient diets. The fourth and fifth columns show the distribution for young inbred Albino rats which were allowed to grow to maturity upon the deficient diets (see Table 1—Diets A, B, C and D). As will be noted the control animals are recorded by totals, only whereas the experimental number of each of the other rats is given. These numbers are arranged on a fertility scale from 100 per cent. down to zero. The small letters after each number designate the particular diet to which that rat was submitted, and an analysis of these diets is given in Table I.

Study of this table (Table II) brings out several interesting facts. The typical fertility distribution for highly fertile animals on a normal diet is shown in the first column. It will be observed that a good 95 per cent. are in the most fertile class; that there are a few animals which are of lesser degrees of fertility and a few more which are sterile.[3]

Column 2, while showing a somewhat similar distribution to the preceding, has more animals which are relatively less fertile. The series is too small to be able to decide on the percentage of actual sterility developed by inbreeding; furthermore when one considers the method

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[3] Post-mortem examinations of these 10 sterile rats showed nothing abnormal except pyometra in 1 female and pus in the seminal vesicles in 1 male.

TABLE II

| 100 | Fert. Distrib. Castle Rats On Stock Diet | Fert. Distrib. King Rats on Stock Diet | Fert. Distrib. of fertile adults on Defic. Diets | Fert. Distrib. of growing King Rats on Defic. Diet | Fert. Distrib. of growing King Rats on special Defic. Diet |
|---|---|---|---|---|---|
| 90 | 1299 individuals | 1, 3, 4, 5, 6, 9, 12, 24, 25, 26, 45, 48, 49, 50, 51, 52, 67, 69, 70, 118, 53 |  | 87a, 95b |  |
| 80 |  | 66, 80 | 3b | 35b, 54b, 57a, 62a, 72b, 97b, 58b, 92a | 122, 123, 125 130 132, 137 |
| 70 | 1 individual |  | 4b, 5b, 26b, 67b, 25b, 48a? | 27b, 36b, 37b, 71b, 74b, 75b, 77b, 83c, 84c, 86c, 93a, 94b, 104a, 59b | 94, 124, 128 |
| 60 |  | 44, 63, 64, 68 | 6c, 12c | 16a, 61c, 76a, 78a, 101a, 103a, 105a | 131 |
| 50 | 8 individuals | 43 | 9c? | 32Fb, 55b, 73b, 88a, 96b, 106b, 107b, 108b, 15c, 21a | 120, 126, 146 |
| 40 | 8 individuals | 65, 79 |  | 28b, 17c, 85a, 99a, 100b |  |
| 0 | 10 individuals | 116<br>Spontaneous variation in fert. of inbred (King) rats | 24b, 50c, 51b, 52c, 69c, 53a<br>Effect of Def. diets on fert. inbred adults | 13c, 14c, 18c, 19c, 20a, 29a, 30b, 32Ma, . 34b, 38a, 39a, 56c, 60c, 81c, 82c, 98b, 102a<br>Effect of def. diets on Fert. of growing inbreds | 119, 121, 127 129, 136, 143<br>Effect of generally def. diet on growing inbreds |

Numbers are experimental numbers assigned individual rats. When followed by a small letter a special diet is indicated; a stands for Diet A., b stands for Diet B., and c for Diet C.

For the explanation of this table the reader is referred to the text.

by which these animals had been bred (only from those selected for vigor) it will be seen that this will be no true guide as to the effect of inbreeding on the production of sterility. Columns 3, 4 and 5 show that the effect of deficient diets upon fertility is greatly to increase the numbers of relatively infertile and sterile animals and this is true for adult animals as well as for growing animals though to a lesser extent. The effects of the individual diets do not vary materially except that the effect of

Diet C, which is defective in two elements, is much greater than for either A or B, which are defective in only one. The diets used with the rats in column 5 were generally deficient and were not specially designed as were Diets A, B and C. They were made up chiefly of cereal products and were lacking in vitamine content and succulence (see Diet D, Table I, for a typical analysis). The kind of dietary deficiency, therefore, is not important. It seems rather to be the degree, since the greater the deficiency the larger the proportion of sterility. The way in which the diet seems to affect sterility is through its general effect on the health of the individuals. The less the effect on health the less the effect on fertility.

## CONCLUSIONS

There may be great individual variation in fertilities. Such variation is increased by inbreeding and by deficient diet. Where the variation is great the amount of sterility is also great. There are individuals whose fertility is so low that they are unable to reproduce with one another but whose fertility remains sufficiently high to allow immediate and successful reproduction with highly fertile individuals. We have formulated a theory of fertility to explain these facts. It may be summarized as follows: The fertility of a mating is the result of the product of the fertility of the two individuals concerned. If this mating fertility is above a certain level the mating is productive; if not, unproductive. This level we have called the Threshold of Reproduction. A fairly large series of further matings and re-matings has seemed to confirm this theory at least in its general aspects. The subject requires further experimental study and it will be interesting to see whether there is any hereditary factor involved in fertility.

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## APPENDIX—BREEDING RECORDS REFERRED TO IN TEXT

*Rat No. 1.* Male—mated with No. 3—young; with No. 80—young; with No. 5—young; with No. 24—no young; with No. 26—young; with No. 32—young. His fertility was estimated to be 95 per cent. more or less since 24 was probably sterile.

*Rat No. 3.* Female—mated with No. 1—young; with No. 6—young; with No. 4—young; with No. 65—no young; with No. 52—no young; with a highly fertile ''Castle'' rat—young. In estimating the fertility of this rat the failures with 65 and 52 must be considered. A reference to their records shows them to be of low fertility, hence 3's fertility is undoubtedly high—perhaps 90 per cent. more or less.

*Rat No. 80.* Was fertile with highly fertile partners but produced no young with less fertile ones. Fertility estimated at 80 per cent. more or less.

Similarly the fertilities of the following rats were estimated from their records: Rat 5 to be 85–90 per cent.; Rat 24—sterile; Rat 26—75–80 per cent.; Rat 68—65 per cent.; and Rat 32—50–60 per cent.

When these estimations are used to check up the record of Rat No. 1, with which they were all at one time mated, they materially help in the estimation of the fertility of that rat (No. 1).

In a similar way the records of the following rats were derived, namely, those of Nos. 13, 17, 72, 73, 99, 100 and 108 (used in the text as illustrations). For instance, No. 17, a male, was mated with a female, No. 13, without young; but when he was re-mated with highly fertile females young were produced in one out of six matings (fertility 40–45 per cent.); but No. 13 did not produce young though mated twice with highly fertile males (fertility below 40 per cent., *i.e.*, sterile).

Again, No. 72, a female, had no young when mated with No. 73; but produced young with two highly fertile males (fertility 70–80 per cent.), while No. 73 impregnated two out of four highly fertile females (fertility 50–60 per cent.).

Rat No. 99, a male, had negative matings with 104, 100, 108 and three out of five highly fertile females. His fertility was estimated at not over 50 per cent.

Rat No. 100 was a female. She had negative matings with males No. 106 and 99; but two out of four matings with highly fertile males were successful. Her fertility was also estimated at 50 per cent. or slightly more.

Rat No. 108 was also a female. She had negative matings with 94 and two highly fertile males. Her matings with two other highly fertile males were positive; and therefore her fertility was estimated to be about 50 per cent. It could be predicted that a mating with No. 99 (also 50 per cent.) would be negative then, and such proved to be the case.

# THE EFFECTS OF ALCOHOL FUMES ON THE ALBINO RAT: INTRODUCTION AND STERILITY DATA FOR THE FIRST TREATED GENERATION

FRANK BLAIR HANSON AND VIRGINIA HANDY
Department of Zoology, Washington University, St. Louis

## The Problem

> One of the outstanding problems of genetics is that of the origin of new heritable variations. With the passage of time, and the accumulation of exact experimental data, it becomes increasingly clear that this factor is the basic one in evolutionary change, whether progressive or retrogressive.—Pearl, 1917.

> There is no a priori reason why the substances of the germ cells should not be as easily altered as any other mass of chemicals. But in practice it turns out that most agents which produce chemical alterations of the germ cells at the same time kill the organism. Further, the germ cells, like other living substances, have a great tendency to compensate for any disturbances induced in them, their condition is one of stable equilibrium, in which an alteration is followed by a return to the original condition.—Jennings, 1920.

Several investigators have attempted to modify the germ cells of mammals and birds by the administration of daily inhalations of alcoholic fumes, ether and other toxic substances. The papers by Stockard ('16, '18) on the guinea pig, Pearl ('16a, '16b, '17) on the domestic fowl, and Cole and Davis ('14) are among the more prominent papers on this subject.

Because of the fundamental character of the problem involved and the conflicting results obtained by two of the workers above mentioned, it seems desirable to repeat this work on a somewhat larger scale, using a different and possibly more favorable animal than has been employed hitherto.

Three aspects of the problem are here considered:

1. *Somatic:* Does the daily administration of alcohol[1] fumes to albino rats from the ages of sixteen days to ma-

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[1] The alcohol used in this experiment was 95 per cent. ethyl alcohol. Hereafter it will be referred to merely as alcohol or alcoholic fumes.

turity produce effects in growth that may be quantitatively measured, and so compared with control animals of the same litter, and with the data on body growth found in Donaldson's ('15) "Book of Reference Tables of the Albino Rat"?

2. *Germinal:* Does the daily administration of alcohol fumes to young albino rats produce alterations in the germ plasm, such as would lead to new heritable variations—either in spectacular abnormalities such as Stockard's guinea pigs showed, or in less evident but definitely measurable variations from the normal growth curve?

3. *Mechanism involved:* Are the somatic effects upon treated animals such as to give any indication of the origin or mechanism of germinal changes; and are the alterations in the germinal materials such as to lend themselves to cytological analysis?[2]

The problem as above outlined is not essentially different from that attacked by Pearl and Stockard. The results of the present authors will be presented in this and subsequent papers.

It is believed that the albino rat offers peculiar advantages in studying those non-spectacular changes which apparently were operative in Pearl's material, and which clearly divided his experimental and control material into two groups, the treated group lacking, however, those striking variations in the form of abnormalities as shown in Stockard's work. As we understand the comparative results of the investigations of Pearl and Stockard, this last-mentioned fact was the chief point of difference between them. They both got definite, but different, modifications as a result of the treatment with alcohol.

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[2] Seventeen months after the experiment started, several of the two original litters were turned over to Professor Caswell Grave for cytological study. Testes and ovaries from the treated animals, and from their control brothers and sisters, were preserved in Allen's B-15 and Bigaud's formalin bichromate. The results of the microscopical investigation are not yet available, but will be published in a subsequent paper by Professor Grave. However, there was a marked departure from the normal appearance in both ovaries and testes of the alcoholic rats. The gross appearance of the controls was normal in every respect.

Our method of attacking the problem differs from theirs in this respect, that they used only adult animals that had previously produced at least one lot of normal young. This was a precaution well taken, but omitted in this experiment for these reasons: It is very important, in our judgment, to determine what are the effects of alcohol in modifying the germ cells of animals long before they reach sexual maturity, for young germ cells, it may be, are more easily affected. In the case of the rat, the control of one normal litter may be safely dispensed with, for the litter is large and the members may be expected to behave similarly to one another as to fecundity and body weight. Therefore, selecting at random from each litter half the animals for the experiment and half for the control, it may be expected that the experimental animals, had they not been treated with alcohol, would have grown and behaved as did their control brothers and sisters. Hatai, in his work, used this method for obtaining control and experimental animals.[3]

Treating the germ cells of mammals with toxic substances from near the beginning of their postnatal life is a new departure from all work of a similar kind in attempting to modify germ plasm.[4]

## REVIEW OF THE LITERATURE

The literature in this field has been reviewed by both Stockard and Pearl. These papers are recent, well known and easily accessible.

It has seemed advisable, therefore, to omit any extensive review of the literature as such, and to refer to papers when needed in the discussion of the data presented.

## MATERIAL AND METHODS

As mentioned above the albino rat was selected as being an animal well adapted for this work. It breeds very rapidly, throws a large litter and in our experience in raising hundreds of these animals there has never occurred an abnormality of any kind. It is a remarkably stable form.

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[3] "This method of comparison is best, since as shown by Jackson the variability of body weight within the litter is only about one half that in the total population." (Hatai, S. '15.)

[4] Since our experiment was started the work of McDowell ('21, '22) has appeared.

Another reason for selecting the rat is that through the labors of Jackson ('13), and especially Donaldson ('15), we are in possession of a body of quantitative data on the normal growth of this animal, such as is not available for any other mammal. By the use of control brothers and sisters of the same litter, and Donaldson's reference tables, it is possible to measure and compare any somatic effects induced during the growth process.

A small colony of albino rats was secured from the Wistar Institute of Anatomy and Biology on October 1, 1920. The females were nearly all pregnant when received.

The animals are kept in clean, comfortable cages. The diet has been a general one of table scraps, dog biscuit and grain.[5]

One of the Wistar Institute females gave birth to her second litter in her present quarters on November 22, 1920. She had thrown a litter of thirteen a few days after being received here, and the second litter contained ten young. Another of the Wistar Institute females gave birth to a litter of ten young on January 7, 1921. The experiment herein reported is based entirely upon these two litters of ten each and their descendants. The sex ratio in the first litter was five males and five females. In the second there were four males and six females. The eyes opened on the fourteenth day, and all the animals were in a vigorous condition, as evidenced by their activity and appearance.

The animals of the first litter were numbered from one to ten, and henceforth will be known by these numbers.[6]

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[5] Some months after the experiment was begun, cooked food was added to the diet. This was made after a Wistar Institute formula, and contained white flour, corn meal, linseed oil meal, mixed grains, salt and milk.

[6] Our method of numbering is a modification of Bell's ('14). As one faces the rat the numbers begin on the outer edge of the rat's right ear. There are five punched places in each ear. Beginning at the reader's left they read 1, 2, 3, 4, 5, on the rat's right ear; and 6, 7, 8, 9, 0, on its left ear. The numbers 3 and 8 are expressed by punches at the tips of the ears.

Those with numbers from six to ten were the treated, the first five served as controls. The second litter was numbered from eleven to twenty, the last five numbers being those of the treated (see text figure 1).

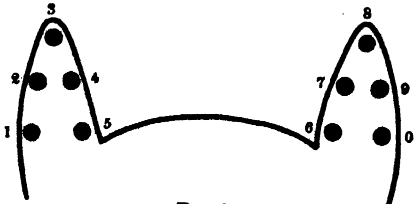

FIG. 1

The rats were weighed individually, to a tenth of a gram, every ten days. The body length and tail length were taken with calipers and these placed upon a millimeter rule to determine the length in millimeters. By a special method of holding the rat the body length was taken in the living animal with very considerable accuracy. All measurements were taken by the senior author with the assistance of a helper in holding the animals.

There was no conscious selection of the animals which were to be controls and those to be treated. The two litters were numbered at random and then divided into two groups, the control group containing numbers one to five and eleven to fifteen, inclusive; the test group with numbers six to ten and sixteen to twenty, inclusive.

TABLE I

A COMPARISON BETWEEN THE CONTROL AND TEST ANIMALS AT THE BEGINNING OF THE EXPERIMENT

| | Body weight (in grams) | | Body length (in mm.) | | Tail length (in mm.) | |
|---|---|---|---|---|---|---|
| | ♂♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀♀ |
| Average of controls | 18.54 | 17.22 | 86.10 | 80.50 | 53.70 | 52.70 |
| Average of tests | 18.30 | 17.28 | 85.25 | 86.08 | 54.25 | 53.91 |
| Average differences | — 0.24 | + 0.06 | — 0.85 | + 5.58 | + 0.55 | + 1.21 |

Table I shows that the two groups of animals differ very slightly. The control males are 0.24 of a gram

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Any combination of figures can be made by this scheme provided the second or third digits of the number is the same or greater than the first, as reading is always from the left to the right. For example, 32 is not possible, for in reading from left to right it would be read 23.

heavier than the experimental males, while the control females are 0.06 of a gram lighter than their sisters. In body length and tail length the two groups are very close together, with the tests a trifle longer in three out of the four groups. It would be difficult to divide the two litters more equally.

The data are quite convincing on two points: (1) The control and experimental animals at the beginning of the experiment were practically identical, the experimental animals having, on the whole, a slight advantage. (2) These two groups are remarkably normal when compared with similar data from Donaldson's tables on the growth curve in the albino rat.

On December 9, 1920, the animals numbered from 6 to 10 (age sixteen days) were put into an airtight chamber in which 50 cc. of 95 per cent. commercial alcohol, poured on cotton, was evaporating. They remained in the fume tank for thirty minutes, and exhibited all the signs of animals whose mucous membrane was seriously irritated. They rubbed the nostrils and sides of the head vigorously with their front feet. They stood on their hind feet, thus extending their heads as high as possible into the chamber to escape the fumes coming from below. Our observations in this respect agree with those of Pearl and Danforth, for there were no permanent effects produced in the eyes of the treated rats. Towards the end of the treatment period the partial loss of control of the hind legs was noticed. When taken out of the tank the young rats were limp, but in the fresh air recovered rapidly.

On January 25, 1921, the second litter (numbers 16 to 20) were treated for the first time. The conditions of the treatment and the reactions of the animals were the same as reported for the first litter.

The fume tank was made from an old incubator by securely stopping all ventilator openings and stripping the edges of the doors with felt. The interior dimensions of the tank are 12 x 15 x 19 inches. The ten[7] animals could be treated at the same time. Figure 2 is a picture of the fume tank.

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[7] Male 16 drowned in the water glass on Dec. 26, 1920; and on Sept. 1, 1921, male No. 8 died of pneumonia, after being treated for nine months.

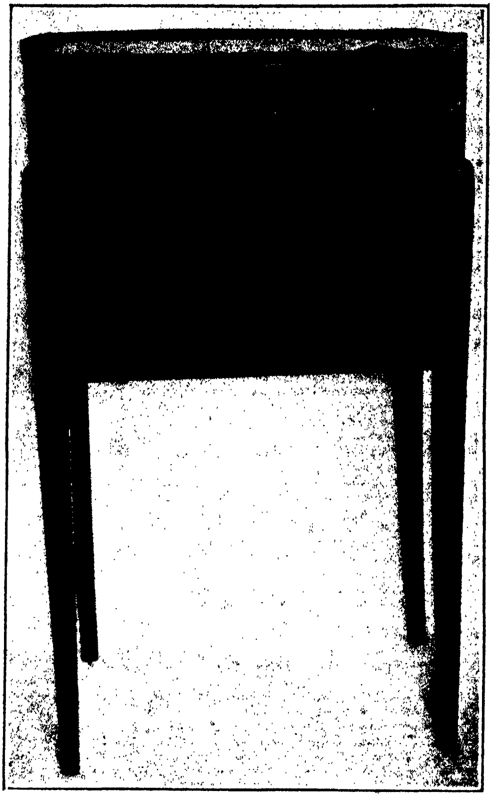

FIG. 2

The two litters lived in the same cage with their mothers until they were thirty days old. At that time each litter was given a larger cage, the two cages being alike in size and appointments. Thus controls and alcoholics lived together until they were sixty-two days old, when each rat was put in a separate but similar cage. Every care was taken to see that the environmental conditions of all 20 animals were the same. The single differential between the control and experimental animals is, without doubt, the alcohol treatment.

## GERMINAL DOSAGE INDEX

Certainly the length of time and the severity of intoxication to which the parents have been subjected should have some effect upon the amount of variation, if any, in the offspring. This was recognized in Stockard's papers, but no definite numerical statements of dosage are given. In their last paper Stockard and Papanicoloau ('18) again mention the importance of the amount of dosage as follows:

> Treating female guinea pigs with considerable doses of alcohol fumes only shortly before and during their pregnancies certainly does not injure the offspring to any noticeable degree. While the same degree of treatment, if administered for months or years, will render these mothers almost incapable of producing vigorous young even when mated with normal males.

Pearl has creditably attempted a numerical valuation of the amount of treatment. He calls this valuation "the total germ dosage index." He proposed this term to designate the number of days during which the gametes, making the offspring zygote, have been exposed to the fumes of the toxic substance.

In our experiment no attempt has been made to give a numerical statement of the amount of treatment. The animals were treated daily (Sundays excepted) until a visible state of narcotization was reached. This, of course, involved several increases in the length of treatment and the amount of alcohol. As resistance developed both the time and the amount of alcohol was increased. The rats of the first generation were treated for twelve months, and by that time could withstand four hours with 200 cc of alcohol in the tank.

## INBREEDING

It has long been supposed that close inbreeding is deleterious to stock of any kind, and abnormalities in strains that show a considerable amount of inbreeding are commonly attributed to that fact. Stockard and Pearl give the exact amount of inbreeding present in their strains. From a survey of his stock reaching back four generations prior to the beginning of the experiment, Pearl concludes that "this stock can not on the average be considered inbred," though it was from a line-bred population, and so to some extent inbred. Stockard and Papanicoloau ('18) state that the alcoholic lines discussed in their paper are practically without inbreeding. Some tables show a slight amount of inbreeding, with no indication of significantly injurious effects. An earlier paper by the same authors seems to show that there were more injurious effects in the alcoholic lines that were inbred than in those that were not.

Castle ('06) inbred Drosophila flies for many generations, his matings all being brother by sister. Fifty-nine generations of this close inbreeding did not injure the fertility of the stock, although there was some reduction in the size of the flies.

Wright ('22) has inbred guinea pigs since 1906, with over 35,000 animals recorded. He reports that "the inbreeding can not be said to have had a specific deleterious effect on general vigor."

Coming to the albino rat, we have a large body of exact data on the effect of one of the closest possible forms of inbreeding (brother-sister within the litter). King ('18a, '18b, '21) has done very exact and conclusive work on the subject. Her experiment has been carried on for over forty generations. "These experiments show that in body growth, in fertility and in general constitutional vigor inbred rats are superior to stock Albinos, reared under similar conditions of environment and nutrition." Miss King's method was brother-sister matings, accompanied by selection.

To summarize: Stockard secured several groups of animals from different dealers and practiced but little inbreeding. Pearl's stock was not essentially inbred, and McDowell's ('21) original stock came from two or more sources.

In the light of the recent work of King, East and Jones, Wright and others, the present authors, instead of avoiding inbreeding, have deliberately practiced it, making all matings brother by sister within the litter. In this way advantage was taken of comparing two groups of animals, tests and controls, that were closely related and approaching homozygosity. In the pedigrees to be presented in a later paper it will be shown that all our animals are traced back to a single pair of rats. The advantages of this are obvious to the geneticist. It might be said that this experiment is now in the fifth generation of treated rats and in no way has inbreeding in our stock shown any ill-effects.

## STERILITY DATA

The daily treatment with alcoholic fumes for the period of a year beyond doubt affected the germ cells. Six alcoholic females were mated October 10, 1921, and in a period of six months only four litters had been born. Four of the six animals never produced a litter. Three of these at no time showed signs of pregnancy. The fourth, number 18, will be discussed later. Number 19 threw a litter on December 19, 1921, with five in the litter. One died on the first day and the rest died four days later. This animal did not breed again, although continuously mated until her death a year later. Female No. 20 produced all the young that carried on the alcoholic line. She threw two litters of normal size and weight, and a third litter of one. This animal was born with a large dark red spot on the back of its neck, evidently caused by a severe hemorrhage, and died on the third day. Forty-three days later alcoholic female No. 20 gave birth to a fourth litter of six normal-appearing young.

Five control females, sisters of the alcoholics, were mated at the same time. One of these proved to be sterile. The four productive controls in the same time produced 12 litters as compared to the five alcoholic litters produced by alcoholic female No. 20. That is, there were 86 control offspring to 26 alcoholics. The one fertile alcoholic, therefore, proved to be a slightly better breeder than the average of the controls.

Number 18, an alcoholic female, showed very different effects from the treatment. From the time of mating (October 10, 1921) to January 7, 1922, she was pregnant three times, and each time the litter was slowly absorbed. She became pregnant again, and on February 1, 1922, she aborted. This was followed by three more absorptions. In June, 1922, this female was taken from her alcoholic mate and mated with a normal male that was known to have sired several normal litters. The following month she gave birth to a still-born litter of one, which was normal in appearance except that it was smaller than the usual size of newborn rats. In fact, it is somewhat doubtful whether this was a late abortion or an undersized full term fetus. No. 18 was mated to normal males until her death November 28, 1922, but showed no further signs of pregnancy.

Of the six treated females of the first generation, therefore, three were rendered completely sterile; one had its germ cells so injured that the single litter it threw died in a few days; one had suffered less injury, but was not able to bring any of her eight litters, with the possible exception of one, to full term; while the sixth produced four litters, of which three were normal.

Both Pearl and Danforth ('19) get a higher percentage of sterility in the treated stock than in the controls. The treated rats appeared no different in life than did the controls; and when killed and examined showed no deposits of fat around the ovaries that would in any way inhibit ovulation. The sterility then must have been occasioned by the treatment with alcohol.

Although our animals were severely treated no abnormalities occurred such as Stockard observed, other than that of the hemorrhage noted above. One alcoholic litter, normal in appearance, died from some unknown cause within four days after birth.

It is commonly believed that after an injury to or alteration of the germ cells there is a tendency for them to revert to their normal condition after the lapse of a greater or lesser period of time. And there is evidence that this is sometimes the case. However, when the injury is severe as in our experiment and the treatment extends over a considerable period of time it seems doubtful if recovery is always made. Five of the alcoholic females were mated for a period of something over nine months after the cessation of the treatment, and one, No. 18, was mated continuously with both alcoholic and normal mates for a year after the treatment ceased, with no evidence of germ cell recovery.

The data for growth in body weight, birth weight, litter size and sex ratio, for five successive generations of alcoholic and test animals are now ready for tabulation and will be published in subsequent papers of this series. The experiment will be continued through the tenth generation according to present plans, and a second series of reports made at the end of the tenth generation. Data secured for the first five generations indicates strongly the wisdom of long-continued experiments upon this important subject of induced changes in germinal materials.

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# THE PSYCHODIDAE (MOTH-LIKE FLIES) AS SUBJECTS FOR STUDIES IN BREEDING AND HEREDITY

C. L. TURNER
Zoological Laboratory, Beloit College

## Introduction

A battery jar containing decaying aquatic vegetation was noticed to contain a large number of midge-like larvae and pupae, and when minute moth-like flies belonging to two different species emerged from the pupa cases the jar was covered to see whether the flies would not breed. The possibility was suggested by the writer having inbred blow flies (*Calliphora vomitoria*) for a number of generations in an unsuccessful attempt to secure mutants. Within a few days it was noted that a new generation of larvae had been produced. These were isolated and a careful record kept of the specimens. Sixteen days after the first adults were seen a new generation of adults emerged from the isolated larvae. From these new adults fresh cultures were started, and after two generations of inbreeding a considerable number of white-eyed mutants were observed.[1] The second species of fly completed its life cycle in a somewhat longer time and produced no mutations. These results demonstrated the feasibility of using the animals for breeding experiments. The two species and the white-eyed mutation have been isolated and maintained as pure strains, the method of inheritance of the white-eyed mutation has been worked out and the reactions of normal and mutant flies recorded. It is intended that the present paper shall be one of a series giving an account of the results obtained.

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[1] The writer is indebted to Dr. J. M. Aldrich, of the United States National Museum, for identifying the two insects described in this paper.

## REQUISITES OF SUITABLE BREEDING ANIMALS

Animals which have proved best adapted for studies in breeding and in life histories have been selected principally for the following reasons:

(1) They have been easily obtained. Rare animals and animals with obscure life histories have sometimes been reared with painstaking efforts, but the very difficulty of obtaining them and of maintaining them has precluded their general use.

(2) They have been easily reared and controlled. The preparation of peculiar media has sometimes presented such difficulties that the raising of the animals has been practically out of the question for general purposes and frequently the necessity of changing or renewing the medium has offered still further difficulties. The ideal animal has been one which could live upon some natural medium.

It has been desirable also that the animals in question be handled with facility. Microscopic animals require the use of a lens in locating them and the use of a capillary pipette or other apparatus in handling them. Larger animals are handled more easily.

(3) They have been relatively small. The consideration of the size of the animal raises the practical problems of housing, feeding and handling. Even such small animals as mice and rabbits when required in great numbers are very expensive to the operator in time, effort and money. Colony houses must be built and the animals must be fed and otherwise cared for. In handling specimens the size is also an important factor. The ideal animal in this respect is one large enough to be seen without a lens and yet small enough to be housed in considerable numbers within a limited space.

(4) They have been animals with a relatively short life cycle. Studies in heredity have been made upon animals whose life cycle extends over several years, but obviously such studies are time consuming and an extensive study involving many generations is a practical impossibility.

An animal which produces several generations a year or a generation every few weeks permits an extensive study within a reasonable period and is much more suitable for general use.

(5) They have had recognizable secondary sexual characters. In counting progeny and in mating pairs the sexes must be readily recognized, and some convenient distinguishing characteristic is a necessity for rapid work.

(6) They have had definite variations in form, color or structure, or have given rise to mutations.

In addition to the above points the ideal animal would require a minimum amount of attention beyond the mating of pairs and the counting of progeny.

In brief, the animals most used for experimental work in breeding are common forms of relatively small size, living upon some natural medium, easily reared and handled, having a short life cycle and either possessing conspicuous variations or capable of giving rise to mutations.

## ADAPTABILITY OF PSYCHODA ALTERNATA AND PSYCHODA MINUTA FOR BREEDING EXPERIMENTS

The details of the life histories of these two Psychodids will be discussed later in this paper, but the features which make them ideal animals for breeding experiments will be taken up here.

(1) They are common insects and are to be found during the entire summer season around sewage, manure piles or decaying aquatic vegetation.

(2) They are easily reared in natural media. Cow dung, horse dung, decaying vegetation and agar made with an old hay infusion as a solvent have been used as media with success. Many generations have been carried through in test tubes and flasks plugged with cotton to keep the animals from escaping. They are easily transferred from one tube to another by making use of their phototropic reactions or by shaking.

(3) They are about 2 mm in length—so small that a hand lens is required at first for distinguishing the sexes. This small size is a disadvantage, but with practise the secondary sexual characters can be made out with the naked eye. The small size is a distinct advantage, however, in the saving of housing space.

(4) *Psychoda alternata* has an extremely short life cycle. At a temperature of 15°–18° C. the life cycle is from 16 to 21 days in length. At 22°–25° C. the average life cycle is from 12 to 15 days in length and at a temperature of from 27°–30° C. the average life cycle extends from 7 to 12 days. Thus there is the possibility of obtaining from 25 to 30 generations in a year.

(5) A mutation which has white eyes and non-pigmented Malpighian tubules appeared in *Psychoda alternata* after the second generation of inbreeding with a normal wild stock. The normal wild fly has reddish-brown eyes and Malpighian tubules, and a reddish-brown ocellus in the larva. In the larval stage the ocellus of the mutant is not pigmented. The mutation was found to behave as a Mendelian recessive and a pure strain is now being maintained.

*The qualifications, in brief, which would recommend Psychoda alternata for breeding experiments are that it is a common insect which may be easily reared in test tubes or flasks in dung or in decaying vegetation. It is capable of producing a generation every 10 to 15 days, under ordinary temperatures. It requires no attention beyond the mating and counting of specimens. It has already given rise to a white-eyed mutation.*

There are some features in the life histories of these Psychodids that are not in their favor as ideal experimental animals. Adult life of sexually mature individuals is of very short duration, and the animals may die before suitable mates can be obtained. Like many other insects the males emerge a day or two in advance of the females and the males may die before the females appear. This can be remedied by forcing the life history to be carrried out in a short space of time when the males and females emerge very nearly together. Specimens copulate soon after they emerge from the pupa case and it is difficult to procure a female which has not already copulated if males are present. This difficulty can be met, however, by isolating specimens in the pupa stage and allowing them to emerge each in a separate tube.

## LITERATURE ON LIFE HISTORY, HABITS AND GENERAL STRUCTURAL FEATURES OF PSYCHODIDAE

The life histories of several species of the Psychodidae have been studied and published. Some of these studies have dealt with limited phases of the life history, while others have been rather complete.

The work of Haseman (1907, 1908) has been the most complete. In his "Monograph of North American Psychodidae" and his "Notes on the Psychodidae" he gives a systematic scheme for identification and descriptions of the various species. He also gives many notes on the life history of the members of the group, including the time that elapses during each stage and the habits during the various stages.

Fullaway (1907) and Welch (1912) give rather full accounts of the life history of three species.

Muttkowski (1915) in his "New Insect Life Histories" describes the larval, pupal and adult stages of one species (*Psychoda cinera*) together with an account of the movements, feeding habits and methods of respiration in the various stages.

Dell (1905) gives a complete description of the external anatomy of all stages of *Psychoda sexpunctata* (a species found in England), and an account of the internal anatomy in the larval and pupal stages. Interesting notes are included on the habits of the larvae and adults relating to their methods of locomotion, feeding and breathing.

Miall and Walker (1895) give descriptions of the external anatomy, life history and habits of another English species (*Pericomia canescens*).

### LIFE HISTORY AND EXTERNAL STRUCTURE OF PSYCHODA ALTERNATA AND PSYCHODA MINUTA

*Adult stage:* The adult insects are about 2 mm in length. The entire body surface and wings are densely covered with long hairs. The mouth parts are rudimentary except for a pair of four jointed maxillary palps. The antennae have thirteen segments, each segment having a bulbous swelling and a whorl of long hairs, while the terminal four segments are small and closely united. There are no ocelli but two compound eyes, dark reddish-brown in color, are present, each bearing about 75 facets. The wings are sharply pointed and are carried in a sloping position. They are fringed with long hairs and each vein forms an axis along which shorter hairs are placed. The abdomen contains nine segments and is slender in the male but swollen in the female. In the male the last segment is flattened, partially bifurcated and bears a long pair of forceps. A smaller pair of forceps borne on the eighth segment is enclosed by the larger pair on the terminal segment. The genital appendages in the female are very small.

*Psychoda alternata* has a light tan-colored body with wings lighter and faintly mottled with black and white. *Psychoda minuta* differs from *Psychoda alternata* in having a uniform dark color on the body and wings, longer hairs and in being more slender in the body, wings and antennae.

The adults of *Psychoda alternata* make rather sustained flights when opportunity offers, but are capable of running about actively and of jumping. The flights of *Psychoda minuta* are short and nervous, and the insect seems to rely more upon running and jumping as a means of locomotion.

Normal specimens of *Psychoda alternata* are positively phototropic for a period after emerging from the pupa case but seem to lose their sensitivity to light after copulation. They are also negatively geotropic. The latter reaction is strong in both normal and in white-eyed mutants, but is of short duration, being confined to the first few hours of emergence. The males emerge in advance of the females and live only for a period of a few days. Females have been observed to live as long as seven days, but this is only in case they have not copulated and have retained their eggs. Normally they do not live so long.

During the reproductive activities the males come into contact with either males or females and after a little preliminary "testing" with the tips of the antennae they extend the forceps forward beneath the abdomen at the same time flexing the abdomen. They attempt to seize the fly with which they have come into contact and if successful will then turn about in the opposite direction but will still cling with the forceps. Males will seize other males quite as readily as they will seize females and one case was observed where males were actively running about seizing each other in a culture in which no females had yet emerged. This would tend to prove that sex recognition does not exist. They will not, however, even try to seize other objects, although males of one species will seize either males or females of another species. The adults are apparently sexually mature at the time of emergence. Copulation was observed in one instance between individuals only forty minutes after they had emerged from their pupa cases.

Dell (1905), after making the observation that the mouth parts are atrophied, states that the flies do not feed in the adult stages (*Psychoda sexpunctata*). Muttkowski in describing the habits of *Psychoda cinera* states that the adults feed continually. The writer has cleared a great many specimens of *Psychoda alternata* in absolute alcohol and xylol and has seldom failed to find a fluid in the alimentary tract corresponding in color to the medium upon which the animals were reared, indicating that there is some active feeding.

*Egg stage:* The eggs are laid in an oval-shaped, gelatinous mass from .5 to 1 mm in length. The eggs are colorless and are arranged irregularly in the matrix. Almost any kind of decaying vegetation, sewage or dung furnishes the necessary chemical stimulus to induce the females to lay their eggs. Under ordinary conditions of temperature and moisture the eggs hatch in a little less than two days.

*Larval stage:* It is in this stage that the animal lives the longest. The young larva is at first entirely colorless but soon develops brown ocelli and a reddish brown pigment in the Malpighian tubules. Still later chitinous plates develop on the dorsal side which are quite brown at first but as the larva grows older they become darker. In addition to the head, which has a heavy chitinous covering, there are eleven body segments, each equipped with short setae. The effective mouth parts consist of a pair of two-jointed, bristled mandibles. The other mouth parts are distinct but rudimentary. The antennae are present as a pair of small knobs. The terminal body segment bears the anus on its ventral side and mounted on a long conical prominence a pair of tracheal openings which are encircled by a whorl of long hairs. Another minute pair of tracheal tubes may be found near the anterior end of the larva, but they do not open to the outside and are apparently functionless.

The alimentary canal is well developed, comprising an esophagus with a pair of salivary glands, a stomach and an intestine. There are no intestinal caeca, but five Malpighian tubules are attached to the intestine. These tubules are quite long in the larva and extend from the anterior to the posterior end of the body cavity being folded at least once.

The life habits of the larvae differ in the various members of the group, but all are alike in being active feeders. Some live under stones in swiftly running, well aerated water and are to be regarded as strictly aquatic. Others are semi-aquatic, living in the decaying aquatic vegetation floating on the surface of lakes and ponds, while other species are still further removed from the aquatic habit, living in decayed tubers and roots. The two species considered in this paper are of the semi-aquatic type. They are capable of living in a pure fluid for a time, but seem to require a solid or semi-solid substratum upon which to move. The posterior end is raised so that the posterior spiracles may obtain air. It is very difficult to drown the larvae as the spiracles may, even if pushed below the water, entrap a bubble of air in the hairy circle about the opening and carry this down with them. Specimens have been submerged for nearly two days without harm to them, but they will eventually drown. Most of the locomotion is accomplished by creeping, but if a specimen is placed in shallow water it will sometimes move by grasping objects at the bottom with its mandibles and pulling itself along while the posterior end continues to be at the surface. The larvae are voracious feeders and devour whatever comes to hand and which they are capable of taking. Small bits of decaying vegetation, living and dead filaments of algae, moulds, sediment and a miscellaneous mass of smaller plants and animals are consumed. The length of the larval life varies greatly with conditions of moisture and temperature. Low temperatures and drying both tend to prolong the life cycle. Haseman found that *Psychoda cinerea* went through a life cycle in from three to five weeks during the late spring and summer while Muttkowski states five to six weeks to be the length of the life cycle in the same species earlier in the season. *Psychoda alternata* completes its life cycle in 8 to 24 days at temperatures ranging from 15° to 30° C. In specimens completing their cycles in 16 days, 10 or 11 days were passed in the larval stage. The maximum size attained by the larva is about 9 mm. No accurate account of the number of moults that take place in the larval stage has been kept, but larval casts measuring six and eight millimeters have been found.

*Pupal stage:* Towards the close of its larval life the insect ceases to feed, becomes sluggish and undergoes the structural changes which convert it into a pupa. The most noticeable external features that arise at this time are the shortening of the entire body and the great differentiation in the head and thoracic regions. The entire chitinous covering becomes darkened, but especially so in the region of the head and the thorax. In *Psychoda alternata* this color may become a dense black while in *Psychoda minuta* it is brownish. The compound eyes arise early in the pupal life and the ocelli disappear. During the pupal life external markings appear which outline the positions of the developing palpi, antennae, legs and wings. The respiratory system becomes radically changed. In the transformation of the abdomen the terminal abdominal spiracles and trachea are lost and a new pair of organs is developed for securing air. A pair of hollow club-shaped organs arises at the anterior end of the body into which the trachea project. There are some other minor changes in the respiratory system. The alimentary canal shortens and differentiates and the Malpighian tubules also shorten.

The abdominal portion of the pupa is capable of movement, but there is little locomotion. The head and thorax are quite rigid and incapable of moving. During the two or three days of the pupal life the animal lies with its respiratory organs projecting from the water or sand and if by any chance these respiratory chambers are completely submerged the pupa will die.

*Period of emergence:* At the conclusion of the pupal stage the pupa case splits along a line between the head and thorax and the adult emerges. The operation of emergence takes about two minutes. The newly emerged specimen has control of its body, with the exception of its wings, and it immediately runs to a dry unobstructed place where the wings unfold. The wings start to straighten out at the base and the process proceeds to the tips, leaving the wings in a vertical position over the animal's dorsal side and parallel to each other. The straightening operation takes about ten seconds.

Within three minutes the wing-hairs become dry and the wings are dropped to their sloping position. The animal then proceeds about its main business of life, namely, reproduction, and has sometimes accomplished this within an hour after emergence.

## CULTURE METHODS

*Media:* A number of different substances have been tried as media. The specimens were first noticed to breed in decaying aquatic vegetation composed principally of Potomogetan. It was recognized that a most successful medium would have to contain whatever chemical substance would induce the female to deposit her eggs and at the same time furnish food for the larvae. A variety of vegetable materials in a decaying condition were tried and all with some degree of success. Maple and oak leaves soaked in water and allowed to decay gave good results. Fleshy leaves—lettuce, spinach, cabbage—after becoming thoroughly broken down by bacteria and yeasts were successfully employed. Tubers and roots occasionally gave good results.

Some investigators have found different species of Psychodidae emerging from old horse and cow dung. These materials were tried as media and have proved so advantageous for the two species described in this paper that other media have been practically abandoned. Both old and fresh dung have been tried, and old dung has given the best results. The material is easily obtained and after being heated in order to kill the eggs or larvae of other insects or of other Psychodidae it may be placed in vessels and supplied with sufficient water.

Another preparation was made by filtering infusions of rotting vegetation or dung and dissolving in this fluid a quantity of agar sufficient to render it viscous. Bits of filter paper were also added to give the adults and larvae a "footing." The females will deposit their eggs readily in this preparation, and when the objective is to observe the animal during the various stages of its life history the medium has the advantage over the natural dung as it is more transparent. Not many individuals come to maturity, however, in this medium, and it is useless where an entire brood must be brought to the adult stage.

*Moisture and temperature:* It is important to have the material upon which the larvae are to feed very moist and yet not covered with water. It will be recalled that the larvae have spiracles at the posterior end of the body which they keep at the surface of the water. Should the material upon which they feed be too deeply flooded the larvae can not keep the spiracles at the surface and at the same time feed. In most flooded preparations the larvae have been drowned after a few days. Ideal conditions are brought about by having the water at such a level that the base of the food mass is flooded and a portion of it projects above the surface. If the culture becomes too dry such individuals as come to maturity are small and weak and a full brood is never produced.

It has already been stated that conditions of temperature affect the length of the life cycle. A number of cultures have been maintained at various temperatures to determine the optimum temperature, one which will cause a life cycle to be passed through in a short time and yet one which would not injure the specimens. 25° C. has proved to be the optimum temperature. At low temperatures the adults are very sluggish and often do not copulate. It seems that the rôle of sight has little to do with the mating of the adults and that they depend upon actually coming into contact. Any agency, therefore, which can concentrate them into a small space and make them more active will promote copulation and insure a fertile culture. At low temperatures the larvae are slow to develop and the time of the life cycle is lengthened. At temperatures higher than 25° C. the adults are active and copulation takes place readily. However, the animals are affected adversely by the heat so that small broods are produced and various fluctuating variations are produced in the adults, such as dark mottlings on the body, short or abnormal wings, hairlessness, etc.

*Culture vessels:* Battery jars have proved to be very satisfactory for housing large mass-cultures. Beyond the renewing of the food material and water at intervals they require but little attention.

For experiments in which an accurate account of each individual must be kept such large vessels as battery jars can not be used. Cultures may be handled in large test tubes or small flasks filled about one third full of moist food material and plugged with cotton. Adults may then be transferred to other tubes and a record kept of the sex and character as each adult emerges. The tubes and flasks have the added advantage of confining the mating specimens to a small space so that contact is assured and copulation is induced. This is especially important in the case of white-eyed mutants. The normal adults are negatively geotropic and have a strong positive phototropic reaction. As a result of these two reactions the normal adults swarm together at the top of the flask on the light side. White-eyed mutants do not have the phototropic reaction and react to gravity poorly. They are reasonably active but have a tendency to remain scattered and in a large vessel they may miss contact altogether.

*Methods of isolating and transplanting:* The adults copulate within a very short time after they emerge from the pupal case and it hence becomes very important to isolate them as soon as they emerge. This is a laborious task and an almost impossible one, for great numbers will sometimes emerge within a very short time. This is of no consequence if the newly emerged adults are not to be mated. If, however, they are to be used for mating they must be isolated before the females have copulated. It has been the practise to isolate specimens desired for mating in the pupal stage, placing the pupa singly upon a wet cotton wad in the bottom of a test tube and plugging the tube with cotton. This insures that the adults when they emerge will not have been exposed.

In transplanting individuals from one culture to another or in obtaining adults from a mass culture it is convenient to place over the culture jar a glass funnel and over the end of the funnel to place a test tube. If a strong light is placed above the tube the flies will react both to gravity and to the light and will pass through the neck of the funnel into the test tube in which they may be transferred.

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# SHORTER ARTICLES AND DISCUSSION

## THE RELATION OF MENDELISM TO MUTATION AND EVOLUTION

It has been generally assumed that Mendel's law of heredity affords a complete explanation of the facts of inheritance. But the characters which conform with Mendel's law, as Mendel understood it, involving dominance and segregation in 3:1 ratios, are comparatively few. They also relate to the more superficial, less important and most recently evolved characters of organisms. Very frequently they consist in the loss of some characteristic of the normal individual and so may be regarded as monstrous or defect variations. The English geneticists have been inclined to regard all Mendelian characters as due to loss variations, but this extreme position is scarcely tenable. Nevertheless, very few Mendelizing variations have a survival value equal or superior to that of the forms from which they have sprung. It is, therefore, probably the fate of most Mendelizing mutations to perish under natural conditions without contributing to racial evolution. But under domestication they are frequently preserved and incorporated in domestic races, if they happen to please man's fancy, which they sometimes do, just because they are distinctive.

The Mendelizing characters of domestic mammals consist very largely of color mutations, such as albinism (an all-white condition), or spotting, or a change from a complex gray and protectively colored coat to a simple black, brown or yellow coat. Other Mendelian mutations involve a change in the length of the hair or the hair slope. The hair may even practically disappear, as in the Mexican hairless dog, due to a Mendelizing dominant character.

Aside from their utility as breed trade-marks, color variations have little value in animal husbandry. The really valuable characters are those affecting size, proportions, rapidity of growth, milk yield, butter-fat content of the milk, wool production in sheep and fecundity, especially in swine and poultry. So far as differences exist between breeds in these important characters, they are not typically Mendelian in inheritance but blending. There is neither dominance nor segregation in recognizable Mendelian ratios when such differences exist between the races crossed. Are they, then, Mendelian? For, if they are not, Mendel's law can not be regarded as the fundamental law of heredity. Very likely they are Mendelian. That is the current interpretation which I see no reason to reject until a better explanation can be substituted for it. (1) It is supposed that in the inheritance of blending characters genetic units (genes) are concerned which are not subject to the law of dominance. Such absence of dominance is known to occur in cases which are otherwise simple and Mendelian in character. (2) It is further supposed that blending characters depend upon the action of more than one gene, usually of numerous genes located in different chromosome pairs, so that they are independent of each other in transmission. The result is that complete segregation is a rare event. (3) It is supposed also that some of the genes on which blending characters depend are more important than others in determining the varying grades of expression of the character. Besides major, there are also minor or modifying factors. Such modifying factors are known to be operative in the inheritance of characters simply Mendelian, but varying slightly in expression.

The important outstanding question concerning evolution is: How do new variations arise? The most popular present-day answer to the question is *by mutation.* This answer, when first given by DeVries, was thought to involve sudden large changes made simultaneously in many characters of the organism giving rise from the start to distinct specific types. This sort of mutation does indeed occur in at least several groups of plants and the mechanism of it is now understood, as a result of the investigations of Gates and others on the evening primroses, of Harrison and others on the roses, and of Blakeslee on the jimson-weed. Such mutation involves variation in the germ cell through duplication of whole chromosomes or through the loss of whole chromosomes, involving as they do simultaneous changes in all characters which have genetic representation in the particular chromosomes duplicated or lost. This kind of mutation can not be regarded as a satisfactory general explanation of the origin of species, the thing which DeVries had in mind when he proposed the theory because comparatively few species differ from each other by whole chromosomes, or are incapable of interbreeding even if they do.

The current theory of mutation, which we owe largely to Morgan, is a theory of evolution by mutation in single genes, not in whole chromosomes. It assumes that changes in single genes occur spontaneously without any as yet known external causes; that change in one gene does not necessarily involve change in any other gene and is usually not attended by it. Each gene mutation will obviously have to stand the test of natural selection and will consequently either be eliminated or will be added to the genetic complex of a surviving race. Intensive study of any species of animal usually reveals the occurrence within it of gene mutations with appreciable frequency. Students of Drosophila have calculated a rate for it in that species. A state of genetic flux may therefore be assumed to be the normal condition in an organism, which assumption corresponds exactly with the view of Darwin that heritable variation is ever present as material for natural selection to act upon. The contrary assumption made in the popular pure line doctrine is quite unsupported by recent critical experimental investigations as well as by the whole science of paleontology.

If each gene, as is apparently the case, is subject to independent mutation, it follows that a blending character, which by hypothesis depends on the joint action of many independent genes, will vary only gradually, since mutation in a gene at a time will produce only minor changes. Mutation in such cases will not be mutation at all except in name, but will consist of a gradual change in the direction favored by selection, again exactly the view of Darwin concerning the usual course of evolution.

The net result of our inventory is to show that Darwin was substantially right in his views concerning the nature of variation and the results of selection, and that the mutationists have lost their case except in so far as they have succeeded in attaching a new name to an old idea.

But we have acquired in Mendel's law a fundamental explanatory principle applicable to all heredity. Yet we must not expect simple three to one ratios to be found in all cases of inheritance or even in any considerable part of them. For only newly evolved characters will conform with it, such as are as yet represented only in a single gene in a single chromosome pair. Older, better established characters, those which characterize the species (rather than a variety), the genus or the class, will have become rooted in many or all chromosomes, and consequently in crosses with other species, genera or classes (when possible) will give a blended result.

W. E. CASTLE

BUSSEY INSTITUTION

# CHROMOSOME ARRANGEMENTS DURING MEIOSIS IN CERTAIN OENOTHERAS

DURING the past two years I have been studying the pollen mother cells of pedigreed strains of the following Oenothera species: *Oe. franciscana sulfurea*,[1] *Oe. biennis*, *Oe. biennis sulfurea*, *Oe. muricata* and *Oe. oblonga*. The following is a brief account of certain meiotic stages in these plants. Fuller descriptions I hope to present in the near future.

I have recently described the reduction process in the anthers of *Oe. franciscana*.[2] Late heterotypic prophase stages in this plant (corresponding to "diakinesis" in most plants) reveal an interesting situation, characterized by (1) a marked tendency on the part of the homologous chromosomes to become paired, a condition quite in contrast to that in most of the Oenotheras so far studied; (2) a constant and definite arrangement of the chromosomes in the nucleus; (3) the association of certain of the chromosomes end to end throughout the period, in such a way as to form a closed circle.

In regard to the first of these characteristics, we find that the species in question differ markedly from one another. On the one hand, *Oe. oblonga* shows a large amount of pairing of homologous chromosomes. *Oe. franciscana sulfurea*, on the other hand, succeeds in forming but one pair; and in *biennis*, *biennis sulfurea* and *muricata*, there is no pairing whatever. With respect to the other two characteristics, however, the plants show a striking uniformity. All present at this stage an arrangement of chromosomes in the nucleus which is constant for the species; and all display at least one large closed circle, consisting of a definite number of chromosomes united end to end. The arrangement of the chromosomes at this stage may be most briefly portrayed in a series of diagrams (see Figs. 1–7).

In the case of *muricata*, the arrangement shown in the figure persists unchanged until metaphase. In *franciscana sulfurea*, the single ring usually breaks away from the large circle, just previous to metaphase; otherwise, the arrangement persists. In *biennis* and *biennis sulfurea*, the typical arrangement (Fig. 2) may become somewhat modified by a separation of the two rings, or by an attachment of the two in such a way as to form a figure

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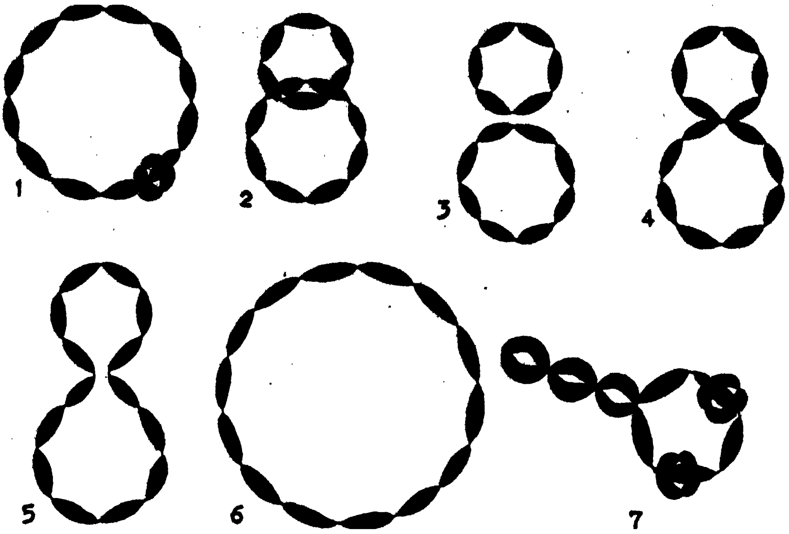
[1] A fuller account of this species is soon to appear in the *Botanical Gazette*.

[2] *Amer. Jour. Bot.*, 9: 391–413. 1923.

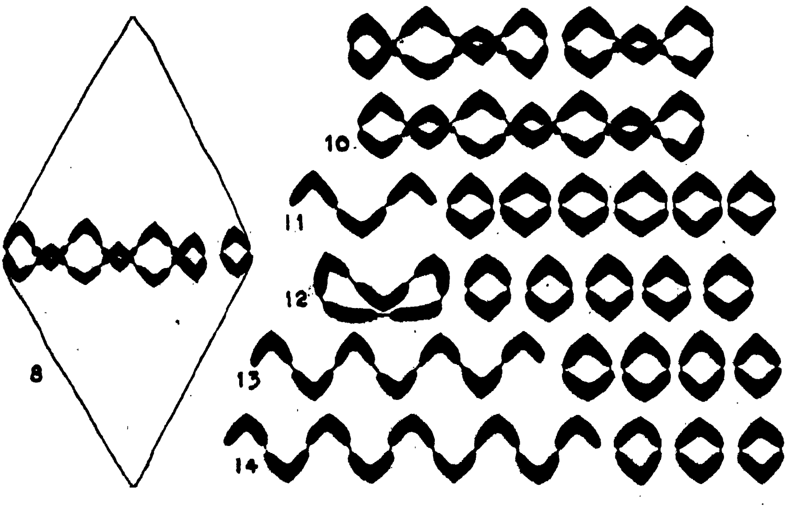


FIGS. 1–8. Diagrams of chromosome arrangements in late heterotypic prophase. 1, *Oenothera franciscana sulfurea;* 2, *Oe. biennis,* typical; 3, 4, 5, modifications of fig. 2: 6, *Oe. muricata;* 7, *Oe. oblonga,* probable complete arrangement.

8, or rarely, by an opening of the latter figure at the point of attachment of the two circles, so that the whole becomes one large circle of 14.

The situation in *oblonga,* a 15-chromosome form, is not so clear, owing to the fact that the chromosomes begin to break apart soon after the second contraction period has past. The complete grouping being rarely seen, therefore, the evidence for a definite arrangement of the chromosomes is not so complete as in the case of the other species. However, I think that the evidence is clear enough to make it fairly certain that the arrangement herewith presented is the correct one (Fig. 7). When the chromosomes separate, and the figure breaks up, the end result is not always the same. It appears that three sets of homologous chromosomes are always formed into definite pairs. In the case of the other chromosomes, however, the affinity between homologues appears to be weaker, and they sometimes succeed in pairing, and sometimes do not. The largest number of distinct pairs that I have observed in a nucleus is six. Such a large number of separate pairs can only be formed by the breaking up of the circle of 5 chromosomes, two of the components pairing. In most cases, however, the five chromosomes which form the circle remain attached throughout this period, and the number of pairs formed is less than six. When the number of pairs formed is less than five, the chromosomes which failed to pair are found still attached to the circle of five, which breaks open, so that chains of seven or nine chromosomes are frequently seen (see Figs. 11–14). In all these species, therefore, there seems to be a definite arrangement of chromosomes in late heterotypic prophase, the arrangements differing in different species, but being constant in each. There is also in each species at least one closed circle, the number of chromosomes composing it varying from four in *franciscana*, to the whole group of fourteen in *muricata*.

Turning now to the heterotypic metaphase, we find that the chromosomes are arranged in the equatorial region as illustrated in the figures (Figs. 8–14). Chromosomes that were attached together in circles or chains in late prophase, are still attached, and those that were separated into pairs are still separated. But the most noticeable feature of this stage is the regular way in which the chromosomes forming the large circles are arranged. With but a small percentage of irregularity, contiguous chromosomes become attached to spindle fibres leading to opposite poles, alternate ones to fibers leading to the same pole. Thus it is brought about that in spite of the fact that the chromosomes fail



FIGS. 8–14. Diagrams of chromosome arrangements in heterotypic metaphase, lateral view. Outline of the spindle omitted except in fig. 8; 8, *Oe. franciscana sulfurea;* 9, *Oe. biennis;* 10, *Oe. muricata;* 11–14, *Oe. oblonga.*

in large measure to pair, but instead, remain attached to one another end to end, they are for the most part distributed evenly and normally to the poles.

The chromosomes in all the Oenotheras that I have studied are so similar in size and appearance that it is impossible to distinguish one from another, and so, by direct observation, determine the exact position of each chromosome pair. However, the uniform linking of groups of chromosomes in each species, and the regular way in which they are arranged in metaphase, and distributed in anaphase, suggests very strongly that the chromosomes making up the circles are not arranged by chance, but have positions in these circles which are definitely fixed. If this were not the case, there would be very little chance that the two members of each of the homologous pairs in the circles would be disjoined in anaphase, by the process employed in these plants. It is more than likely, therefore, that the chromosomes are placed in such a way in the circles, that homologous ones are separated to opposite poles. Bearing in mind the condition found in metaphase, the most natural arrangement allowing of such a result is an end to end relation between the homologous chromosomes, and this I believe is in all likelihood the actual condition. If we assume the probability that within the larger groups of chromosomes there is a constant arrangement of the homologous chromosomes into pairs, it is but an easy step to the further assumption that the chromosomes are not only arranged into pairs, but have definite positions within the pairs also. Thus the arrangement AA′ BB′ CC′ (representing three adjacent pairs of homologous chromosomes) should not, except through irregularity, become AA′ B′B CC′.

Supposing, then, that the chromosomes are thus fixed in their position in the circle, it follows clearly that the group as a whole constitutes a unit, both structurally and in behavior, acting very much like a single chromosome pair. Chromosomes ABCD normally go to one pole, and A′B′C′D′ to the other. Chromosomes ABCD are then as much linked in effect as though they were merely parts of a single chromosome, the homologue of which is composed of A′B′C′D′.

The possible bearing of this situation upon the experimental work of Shull[8] in which he finds evidence of a large amount of character linkage in the Oenotheras, need only be mentioned. Shull finds that most of the characters that he has studied so far seem to belong to the same linkage group. He believes, therefore, that the genes for all of these characters are carried in the same chromosome pair. In view of the facts here presented, it seems to me that the possible correspondence of larger units composed of several chromosomes, rather than of individual chromosome pairs, to character linkage groups such as Shull has discovered, should be kept in mind.

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[8] *Eugenics, Genetics and the Family,* Vol. I, pp. 86–99, 1923; *Genetics* 8: 154–167, 1923.

RALPH E. CLELAND

GOUCHER COLLEGE

## THE INGESTION OF CHLOROPHYL BY ANIMAL CELLS

WHILE the experiments on tissue cultures carried on in this laboratory for the past few years have shown that the connective-tissue cells of the chick embryo are able to take in a wide range of foreign bodies, nevertheless it is rather startling to be able to cause animal cells to become as green as any plant cell simply by placing them in an environment containing chlorophyl.

The size of the chlorophyl droplets formed in the animal cell depended upon the method of preparing the chlorophyl and varied from almost ultramicroscopic yellow green particles to large blue green droplets about the same size as the fat droplets native to the cells.

Chlorophyl obtained by boiling crushed plant (grass or spinach) tissue was toxic and this method was soon discarded, even though when a trace of this was added to the medium of the tissue cultures very minute green globules later appeared in the cells. Plant juice undergoes rapid and marked changes upon exposure to the air and becomes toxic, not only for animal tissue but also for plant cells. This has proved one of the great hindrances to obtaining plant tissue-cultures, for while almost any animal tissue exhibits some growth, however slight, in plasma cultures, plant tissue is rapidly killed when placed in plant juice.

If the plant juice was crushed in 95 per cent. alcohol a deep blue green transparent solution resulted which was not at all poisonous to animal cells, provided the alcohol was diluted or driven off by heat. When the alcoholic extract was added to the tissue culture medium (Locke-Lewis solution, Lewis and Lewis, 1915),[1] it formed a slightly turbid solution containing chlorophyl in very minute globules. The cells of a 24 hour growth of embryonic chick connective tissue, bathed in such a solution containing not more than 1 per cent. alcohol, became (after 20 hours) a pale yellow green color due to the inclusion of a great many very small green globules. A much stronger emulsion of chlorophyl was obtained by adding 25–50 per cent. of the alcoholic extract to the medium and then holding a flame over it until the alcohol was burned off. This procedure left a deep blue green scum over the solution which broke up into globules upon cooling. This scum was drawn off and stirred in fresh medium until an emulsion of green globules about the size of yolk globules was formed. This was placed on cultures of connective tissue and was rapidly taken in by the cells, so that after twenty hours the cells contained many deep blue green globules of different sizes scattered through the cytoplasm.

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[1] Lewis, M. R., 1918, *Science*, XLVIII, 398.

As has been shown in regard to other foreign bodies the clasmatocytes exhibited the greatest avidity in the ingestion, often becoming so full of green globules that the other structures of the cell were obscured.

The behavior of the embryonic chick connective tissue in vitro toward these green globules was the same as they exhibited toward other foreign bodies, especially fat globules (Smith, 1921;[2] Lewis, 1918).[3] There were no purposeful movements exhibited by the cell toward the chlorophyl globules or vice versa. The contact between the foreign body and the cell took place entirely by chance. The cells made no effort to engulf the globules and no cell processes flowed out around them. In a few instances a vacuole was formed around one or a group of the chlorophyl globules. Little digestion of the chlorophyl took place, although occasionally some of the globules become yellow green and faded out, as though digestion had occurred. No green color appeared in any of the mitochondria nor were the chlorophyl globules ever attached to the mitochondria.

Cultures containing cells which had ingested chlorophyl lived as long as the controls, in some sets of experiments even longer, but no particular benefit to the cells was noted; they lived, divided and degenerated about as usual.

MARGARET REED LEWIS

JOHNS HOPKINS MEDICAL SCHOOL

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[2] Lewis, M. R. and W. H. Lewis, 1915, *Amer. J. Anat.*, XVII, 339.

[3] Smith, D. T., 1921, Johns Hopkins Hosp. Bull., XXXII, 240.

# CYTOLOGICAL STUDIES IN THE GENERA RUBUS AND CRATAEGUS

CYTOLOGICAL investigations of known hybrids by European and American investigators have shown that hybrids can be separated from more stable species by their chromosome behavior at meiosis. Some authors even have been able to use this character to distinguish $F_1$ hybrids from hybrids of later generations.

The present cytological studies were undertaken in order to determine if some irregularity in the chromosome distribution of the pollen-mother-cell, during its development, would not explain the reproductive sterility so general in Rubus and Crataegus.

Based on studies of the pollen-mother-cell development in 36 species and forms of Rubus, and 81 of Crataegus, I sum up the situation as follows:

The Rubus can be divided into two major classes:

(1) Diploid species, in which I find the gametophytic chromosome number to be 7, the sporophytic 14.

(2) Polyploid species, including triploid, tetraploid, pentaploid, hexaploid and octoploid.

The diploid Rubi are characterized by a regular distribution of chromosomes and regular pollen formation. This, I consider, is a pretty reliable criterion of a homozygous species.

The polyploidous species are characterized, not only by an increase of chromosomes above the diploid number, but by striking irregularities in chromosome distribution and irregular pollen formation frequently leading to polycary and polyspory. In view of the similarity of these irregularities to those found in known hybrids, I consider that this group is made up of heterozygous species and forms.

The Crataegi can be divided into three major classes:

(1) Diploid species, in which I find the gametophytic chromosome number to be 16.

(2) Triploid and tetraploid species that are able to develop their pollen-mother-cells to the tetrad stage.

(3) Triploid and tetraploid species in which the pollen-mother-cell is thin and vacuolated and seldom develops to the tetrad stage.

The diploid Crataegi are characterized by a normal pollen formation.

The triploid and tetraploid species that are able to form pollen show irregularities in their chromosome distribution that frequently leads to polycary or polyspory. These characters are clearly of the type associated with heterozygous species.

The triploid and tetraploid species that are unable to form pollen represent hybrids that are unable to reproduce themselves and have resulted from crosses of distantly related species.

The diploid species of Rubus and Crataegus can be compared advantageously with the stable diploid species of Rosa as recently studied by Täckholm, and the stable *Oenothera grandiflora* and *O. franciscana* of the Onagraceae.

I have found polyploidous Rubi and Crataegi very general. This cytological study, substantiated by morphological and genetical studies, has shown the hybrid nature of a large number of species in these two polymorphic genera.

These heterozygous forms show the following characters: pollen sterility, variability of offspring, polyploidy, irregular chromosome distribution, polycary and polyspory—features all clearly associated with hybrid forms.

It seems, therefore, reasonable to conclude that in these two polymorphic genera, multiplication of species has taken place by hybridization in their natural habitats. Some hybrids may date back to preglacial times, but there is much evidence to show that many of the so-called species originate at the present time wherever inter-fertile species are present.

ALBERT E. LONGLEY

LABORATORY OF PLANT MORPHOLOGY,
HARVARD UNIVERSITY

## A GYNANDROMORPHIC BEE OF THE GENUS OSMIA

IN going over a collection of Osmias from the Rocky Mountain Region belonging to the American Museum of Natural History, an interesting gynandromorphic specimen was found. Although such phenomena have been frequently mentioned and discussed[1] as occurring in other genera, the occurrence is very unusual for this genus. In the key to the females of this region this specimen runs to *Osmia pentstemonis* Cockerell from which it differs only in having the legs dull black and not at all metallic as is true of *pentstemonis*; so the writer has assigned it to this species.

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[1] See Morgan, T. H., "The Physical Basis of Heredity," pp. 189–93; also Cockerell, T. D. A., "Zoology," pp. 85–6. The only reference to a gynandromorphic Osmia which the writer was able to find occurs, page 91, "Die Hermaphroditen und Gynandromorphen Hymenopteren," by K. W. v. Dalla Torre and H. Friese.

This specimen was referred to *Osmia caerulescens* L. and is described as having the head mainly female, with the exception of the pubescence of the left side of the clypeus; thorax and abdomen male, but bluish as in the female; legs entirely male; abdomen with seven segments; genital organs apparently male.

The following characters were noted: About 8–8.5 mm long; bilateral division apparent in the head and abdomen, but no apparent division in the thorax; the male characters occur on the right side and the female on the left. Right side of head brassy green with white hairs; antenna with thirteen joints, dark ferruginous beneath; mandible bidentate; cheek with black hairs above and some white hairs below. The vertex does not show such distinct division, but is bluish with black and white hairs intermixed. Left side of head blue with black hairs, which are almost true bristles; more coarsely punctured than the right side; antenna with twelve joints; mandible tridentate; hair of cheek entirely black. Thorax dark greenish blue; mesothorax and scutellum with punctures hardly the diameter of a puncture apart, shining between punctures; pubescence largely white with some black hairs intermixed; hair of pleurae apparently light, but badly worn; tegulae black. The sculpturing of the abdomen is similar on the two sides, but otherwise the sexual characters are clearly defined on each side. Right side of abdomen brassy green with pure white pubescence; apical segment somewhat emarginate at the side as in *eutrichosa* Cockerell, with a tuft of longer hairs at the side. Left side of abdomen blue with black pubescence; ventral scopa black. Wings faintly dusky; anterior wing 6.25 mm long; basal nervure slightly in front of the nervulus; marginal cell slightly fuscous; left wing with the second recurrent nervure reaching the second submarginal cell nearer the apex than in the right wing. Legs black, with pubescence largely dark.

Habitat: Peaceful Valley, Colorado, June 18, 1922, on dandelion (*Taraxacum*), (Dorothy Young). Collection American Museum of Natural History.

GRACE ADELBERT SANDHOUSE

UNIVERSITY OF COLORADO

## THE BEE-EATING PROCLIVITY OF THE SKUNK[1]

IN the August number of *Gleanings in Bee Culture*[2] for 1923,

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[1] Contributions from the Entomological Laboratory of the Bussey Institution, Harvard University. No. 229.

[2] Published by the A. I. Root Company, Medina, Ohio.

Mr. Geo. S. Demuth, one of the editors, (p. 546) has the following to say concerning the relation of the skunk (*Mephitis*) to *Apis mellifica:* "Skunks are sometimes quite destructive in the apiary. They scratch at the entrance to entice the bees to come out, and then eat them in large numbers. Apparently these animals have no fear of stings or have some method of eating the bees without being stung." In this connection the following observations may be of sufficient interest to be worth recording.

During the summer of 1923, while working on the biology of bumblebees, I had under observation about sixty *Bremus* (*Bombus*) colonies, of which all but one were kept in situations where they could not be molested by ants, the single exception being a colony of *Bremus fervidus* which had been transferred to the Bussey Beeyard and placed beneath a table on which a colony of hivebees was kept. On the morning of August 21, I discovered that the nest-box of this bumblebee colony had been completely cleaned out—apparently by some mammal—with the exception of a few shreds of cotton and about a half a dozen workers which were eagerly searching for their brood. For the benefit of these five or six workers, another *fervidus* colony, consisting of a queen and about thirty workers, was transferred to the spot. However, three days later (August 24), I found that this colony also had been completely destroyed during the preceding night. I therefore decided to ascertain the identity of the marauder, and in the evening set a trap baited with bumblebee comb. To my great satisfaction, I found a half-grown skunk in the trap on the following morning. Being interested to know how this animal is able to dispose of a whole bumblebee colony, apparently without being stung, I decided to keep it to see whether I could not make some observations on its bee-eating habits.

For this purpose the skunk was provided with a special domicile composed of two adjoining boxes, each measuring about 2 x 2 x 2 feet, one of which may be called compartment No. 1, and the other, compartment No. 2. Compartment No. 1, which was partly filled with hay, was completely closed, with the exception of a small opening (about 6 x 9 inches) which communicated with compartment No. 2, while compartment No. 2 was provided with a layer of sand and sawdust, and with a wide-mesh wire cover. In this way, I was able to place food in compartment No. 2 without running much risk of being sprayed, for the animal habitually spent the day in compartment No. 1 and prowled about in compartment No. 2 at night, and it was also possible to make the following observations on its bee-eating habit.

On August 27, a colony of *Bremus fervidus,* consisting of a queen, about fifty workers, and some brood, was placed in compartment No. 2 shortly after dark (about 8 P. M., daylight-saving time). I waited until about 9 P. M., but the animal refused to leave its den (compartment No. 1). However, when I returned about a half an hour later and turned on my flashlight, the skunk was greedily eating a piece of comb containing brood in compartment No. 2. He did not seem to like this intrusion, however, for he immediately stopped eating and returned to his den. Under these circumstances it seemed best to discontinue my observations for that night. When compartment No. 2 was examined the next morning, nothing was left of the *fervidus* colony and nest, excepting a few shreds of cotton.

I now became interested to know whether a skunk can also overcome large bumblebee colonies. A nest of *Bremus impatiens,* containing at least 200 workers and numerous queens and males, was therefore placed in compartment No. 2 on August 28, shortly after dark. To my astonishment, this colony also was found completely destroyed on the following morning. This remarkable feat aroused my curiosity still more, and I decided to make a second attempt to see whether I could not find out how the skunk accomplishes such a hazardous task, for, according to my experience, half a dozen bumblebee stings are sufficient to put the average person to bed for a day or two.

In order to keep the animal from returning to its den after entering compartment No. 2, the sliding door between the two compartments was attached to a pulley so that the opening by which the two compartments were joined could be closed without much noise. After making this change, a colony of *Bremus impatiens,* consisting of about 75 workers, a few queens and males, and some brood, was placed in compartment No. 2 on August 30, shortly after dark. At about 8 P. M., the skunk entered compartment No. 2, whereupon the door between the two compartments was closed. When I turned on one of my two flashlights, the animal again tried to slink back into its den, and, finding the door closed, worked for over an hour at the latter trying to get back into compartment No. 1. However, about 9:15 P. M. the skunk suddenly turned his attention to the bumblebee colony, and now the following, at times exceedingly comical, "melodrama"—the "music" was supplied by the bees—was enacted within two feet of my flashlights:

The first thing the skunk did was to scratch at the nest. This was immediately answered by a shrill chorus from within. As the workers came rushing out, they were seized one by one with one of the front paws, rolled on the ground for a few moments with a quick, alternating, back-and-forward movement of both paws, and then eaten with a crunching noise. At other times, the skunk would seize a piece of cotton with which the bees had covered their comb, roll it in the manner described, and then examine it to see whether it contained any bees. However, every once in a while he would make a frantic jump as a result of being stung by some worker which had eluded him. Such bees were usually seized directly with the teeth and eaten without being rolled. From time to time, the skunk tried to get at the comb, but in this he did not succeed until he had disposed of about half of the bees, when he quickly seized some of the brood, and after having carried it into a corner, began to devour it with much relish. While thus engaged, he was several times painfully interrupted by prowling workers. After he had consumed this chunk of brood, he returned to the nest, and after having disposed of several more bees, took out another piece of comb and ate it. By 10 P. M., all of the bees and comb had been disposed of in this manner, excepting one or two workers and several males which had made their escape by crawling through the wire cover of compartment No. 2. On one or two occasions, I saw him eat a male without rolling, but he invariably rolled the queens. When one of the latter accidentally fell into his water dish, he fished her out with one of his front paws and then treated her in the same manner as the others.

In the evening of September 1, this experiment was repeated before several students and a member of the faculty of the Bussey Institution with a somewhat larger colony of *Bremus impatiens*. Although the skunk failed to work as well on this occasion as two nights before, he had disposed of about a fourth of the colony and brood by 10 P. M., and by the next morning nothing remained of this colony and nest, except some cotton, a few empty cocoons and six or seven numb workers. On this occasion, the skunk was stung more frequently than on the preceding, but apparently without any ill after-effects, for on the following day (September 2) he readily ate beetles, crickets, grasshoppers, moths and even full-grown woolly bear caterpillars (*e.g., Arctia acraea;* det. Dr. A. L. Reagh). Of these insects, the woolly bears were rolled in a similar fashion as the bumblebees, but longer and more leisurely. The beetles, crickets, grasshoppers and moths, on the other hand, were consumed without this treatment. The non-insect part of a skunk's bill of fare seems to be well known,[3] and I shall therefore not discuss my rather scanty observations along this line.

In addition to the bumblebee colonies which were destroyed in the Bussey Beeyard, I found a considerable number of despoiled *Bremus* and *Vespa* nests in and near the Arnold Arboretum, all of which but one[4] bore distinct earmarks of having been destroyed by skunks.

## SUMMARY

(1) The skunk is an important enemy, not only of the hivebee, but also of bumblebees and probably also of social wasps.

(2) The skunk fears stings, but the latter do not seem to have very serious after-effects.

(3) When robbing a bumblebee colony, the skunk makes most of the bees harmless by rolling them on the ground and then eating them.

O. E. PLATH

BOSTON UNIVERSITY

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[3] Cf. Detlefsen, J. A. and Holbrook, F. M. "Skunk breeding with notes on mutations and their genetic behavior." *Journal of Heredity,* Vol. 12 (1921), pp. 243–254, 8 figs.

[4] This nest was a surface nest of *Bremus fervidus* and was probably destroyed by a crow or some other bird.

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